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MELBOURNE

THE DISTRIBUTION AND BIOLOGY OF THE GENUS *AHAMITERMES* (ISOPTERA)

By J. H. CALABY*

(*Manuscript received May* 7, 1956)

Summary

The little-known Australian genus, *Ahamitermes*, contains four described species: *A. nidicola* Mjöberg (Queensland), *A. hillii* Nicholls (south-western Australia), *A. inclusus* Gay (restricted to a small sub-coastal area in mid-Western Australia), and *A. pumilus* (Hill) (New South Wales and Western Australia). Many new distribution records of *A. hillii* and some of *A. inclusus* are given.

New observations on the biology of *Ahamitermes* show that the various species have a species-specific parasitic nesting relationship with either one of two species of the genus *Coptotermes*. They live in specific parts of the inner sections of *Coptotermes* nests, utilizing as food the carton composing these sections, and are thus dependent on the host for food and shelter. They are not found in any other situation. The nests of host and parasite are separated and the two species are mutually hostile. *A. pumilus* differs from its congeners in that it is also dependent on the host for the release of its alates which are tolerated inquilines in the host's nest.

Termite associations in general and that of *Ahamitermes* and *Coptotermes* in particular are discussed.

I. INTRODUCTION

The genus *Ahamitermes* which is known only from Australia, and even here considered to be very rare, contains four species of termites with rather unusual nesting behaviour.

In his monograph of the Australian termites, Hill (1942) recorded three species known from few series. The biological data he was able to record were very meagre. He stated that the species lived exclusively in the nests of *Coptotermes*, two species (*A. nidicola* Mjöberg, 1920, and *A. hillii* Nicholls, 1929) being found in galleries in the outer wall, and the third (*A. pumilus* (Hill), 1942), known from only a single series, in the nursery and other galleries of a populous colony of *C. acinaciformis* in the interior of a living tree.

In recent years much new material of this genus has been collected in Western Australia, including a fourth species (*A. inclusus* Gay, 1955) and complete nest series of *A. pumilus*, the alate caste of which was unknown. Gay (1955*a*, 1956) has given brief details of the biology of these two species. Detailed examination of nests of the three species occurring in Western Australia has made it possible to record here a more complete account than hitherto of the relationship existing between species of *Ahamitermes* and *Coptotermes*.

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The known distribution of all species of *Ahamitermes* is shown in Figure 1. A representative collection of all specimens mentioned in this paper is housed in the Division of Entomology Museum, C.S.I.R.O., Canberra.

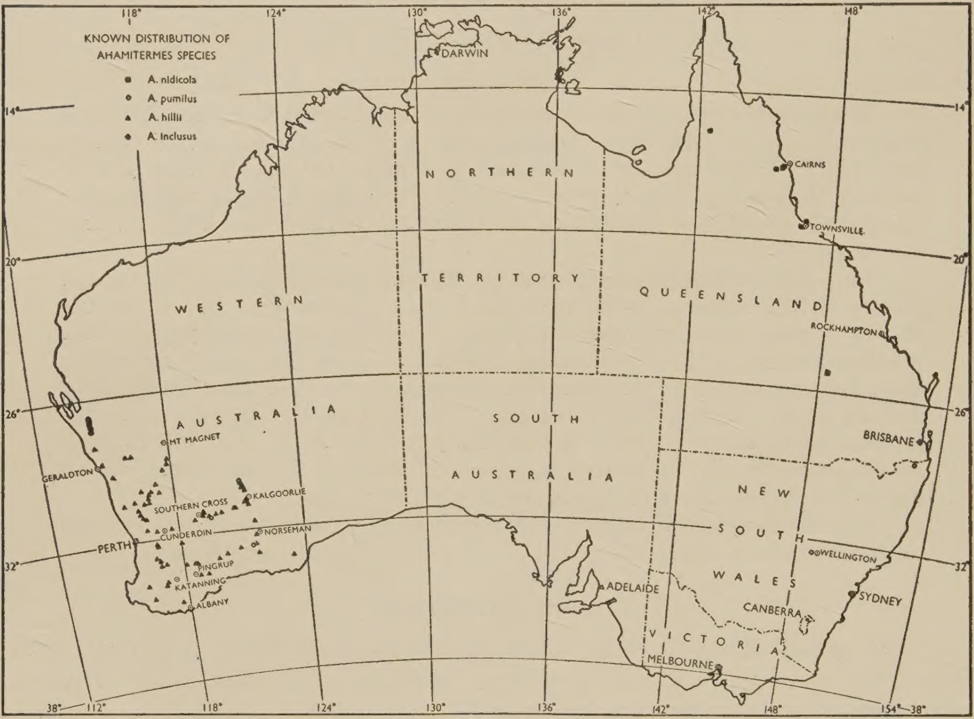

Fig. 1.—Map showing known distribution of *Ahamitermes* species.

II. A. NIDICOLA

No further information on *A. nidicola* has come to light since Hill (1942) recorded eight series, all from Queensland and all taken from galleries in the outer clay wall of nests of *C. acinaciformis* (Froggatt). The actual nest of *A. nidicola* has not been described but it will probably prove to be similar to those of *A. hillii* and *A. inclusus* described in this paper.

III. A. HILLII

(*a*) *General*

A. hillii is known from south-western Australia from which region Hill (1942) recorded five or six series from five localities. Recent collecting has shown the species to be quite common and it has been collected at many new localities. As it lives exclusively in the nests of *C. acinaciformis,* its distribution would, of course, depend upon that of its host, and in fact it has been collected in all areas where the host has been studied intensively. During a trip in 1954, the chief object of which was the collection of *Coptotermes* for a study of the taxonomy and biology of that genus, of 78 randomly selected mature nests of *C. acinaciformis* examined, 32 (41 per cent.) were found to harbour colonies of *A. hillii*. A similar trip in 1955 to a different area yielded 18 colonies (38 per cent.) of *A. hillii* from 47 mature nests of *C. acinaciformis*.

The known distribution of *C. acinaciformis* in Western Australia is recorded in a recent paper (Calaby and Gay 1956).

(*b*) *Distribution Records*

New records of *A. hillii* are as follows: Ajana, 2 miles W. of, 27.x.55 (J.H.C. and F. J. Gay), soldiers, workers; Bardoc, 3 miles SSE. of, 27.x.54 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Bardoc, 9 miles NW. of, 27.x.54 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Beverley, 10 miles SW. of, 27.ii.53 (2 series) (J.H.C.), alates, soldiers, workers, and soldiers, workers; Bilbarin, 8 miles E. of, 5.iv.53 (2 series) (J.H.C.), alates, soldiers, workers, and soldiers, workers, nymphs; Brookton, 9 miles WSW. of, 20.x.54 (J.H.C. and F.J.G.), queen, king, soldiers, workers, nymphs; Bulla Bulling, 5 miles WSW. of, 29.x.54 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Bulla Bulling, 9 miles WSW. of, 29.x.54 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Bungulla, 3 miles E. of, 1.xi.54 (J.H.C. and F.J.G.), neoteinics, soldiers, workers; Buntine, 4 miles NNW. of, 20.iii.53 (J.H.C.), soldiers, workers; Calingiri, 11 miles WSW. of, 21.vii.55 (D. H. Perry), queen, soldiers, workers, nymphs; Carrabin, 2 miles E. of, 31.x.54 (J.H.C. and F.J.G.), soldiers, workers; Coolgardie, 7 miles NE. of, 26.x.54 (J.H.C. and F.J.G.), queen, king, soldiers, workers; Coolgardie, 8 miles NE. of, 26.x.54 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Coolgardie, 9 miles NE. of, 26.x.54 (J.H.C. and F.J.G.), soldiers, workers; Dale River, near Beverley, 21.iv.55 (J.H.C.), soldiers, workers; Dalwallinu, 1 mile S. of, 18.x.55 (J.H.C. and F.J.G.), soldiers, workers; Dandaragan, 11 miles NNW. of, 29.x.55 (J.H.C. and F.J.G.), soldiers, workers; Daniell, 23.x.54 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Dryandra, 6.iv.55 (J.H.C.), alates at lamp; Dryandra, 6 miles NW. of, 20.iv.56 (J.H.C.), alates, soldiers, workers; Dryandra, 3 miles W. of, 14.vii.55 (J.H.C.), soldiers, workers; Geraldton, 8 miles NE. of, 17.iii.53 (J.H.C.), alates, soldiers, workers; Goongarrie, 3 miles S. of, 27.x.54 (2 series) (J.H.C. and F.J.G.), soldiers, workers, nymphs; Higginsville, 5 miles NNW. of, 25.x.54 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Highbury, 2 miles SSE. of, 30.x.53 (J.H.C.), soldiers, workers; Jingalup, 9.x.53 (J.H.C.), soldiers, workers; Kalannie, 14 miles N. of, 28.iv.53 (J.H.C.), soldiers, workers; Karalee, 2 miles E. of, 29.x.54 (J.H.C. and F.J.G.), soldiers, workers; Karalee, 8 miles E. of, 29.x.54 (J.H.C. and F.J.G.), soldiers, workers; Karalee, 2 miles W. of, 29.x.54 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Kukerin, 4 miles NE. of, 21.x.54 (J.H.C. and F.J.G.), soldiers, workers; Kojonup, 3 miles N. of, 30.xi.54 (J.H.C.), soldiers, workers, 17.iii.55 (J.H.C.), alates, soldiers, workers; Lake Grace, 26.iv.41 (F. N. Ratcliffe), alates, soldiers, workers; Lake Grace, 7 miles ESE. of, 21.x.54 (J.H.C. and F.J.G.), soldiers, workers; Lake King, 34 miles ENE. of, 22.x.54 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Lake King, 10 miles E. of, 22.x.54 (2 series) (J.H.C. and F.J.G.), soldiers, workers, and soldiers, workers, nymphs; Manjimup, 16 miles SSE. of, 5.iii.53 (J.H.C.), alates, soldiers, workers; Miling, 8 miles E. of, 18.x.55 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Moorine Rock, 3 miles ENE. of, 31.x.54 (J.H.C. and F.J.G.), soldiers, workers; Mt. Ragged, 15 miles NNW. of, 18.xi.47 (T. Greaves and J.H.C.), soldiers, workers; New Norcia, 6 miles NNE. of, 18.x.55 (J.H.C. and F.J.G.), soldiers, workers; 90-Mile Tank (*c.* 65 miles ENE. of Lake King), 21 miles ESE.

of, 23.x.54 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Noongaar, 2 miles E. of, 31.x.54 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Norseman, 11 miles SSW. of, 24.x.54 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Northam, 8 miles WSW. of, 1.xi.54 (J.H.C. and F.J.G.), soldiers, workers; Paynes Find, 15 miles NNE. of, 20.x.55 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Paynes Find, 30 miles NNE. of, 20.x.55 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Paynes Find, 31 miles NNE. of, 21.v.53 (J.H.C.), soldiers, workers, nymphs; Paynes Find, 8 miles W. of, 20.x.55 (J.H.C. and F.J.G.), soldiers, workers; Paynes Find, 9 miles W. of, 20.x.55 (J.H.C. and F.J.G.), soldiers, workers; Paynes Find, 13 miles W. of, 19.x.55 (J.H.C. and F.J.G.), soldiers, workers; Pindar, 9 miles E. of, 22.x.55 (J.H.C. and F.J.G.), soldiers, workers; Pingrup, 16 miles E. of, 3.ii.53 (J.H.C.), alates, soldiers, workers; Pingrup, 37 miles E. of, 31.x.53 (J.H.C.), queen, soldiers, workers; Pithara, 5 miles SW. of, 18.x.55 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Salmon Gums, 2 miles S. of, 24.x.54 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Southern Cross, 7 miles SSE. of, 30.x.54 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Southern Cross, 8 miles NW. of, 30.x.54 (J.H.C. and F.J.G.), soldiers, workers; Southern Cross, 11 miles NW. of, 30.x.54 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Southern Cross, 12 miles NW. of, 30.x.54 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Strawberry, 28.x.55 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Walebing, 3 miles SSE. of, 28.viii.53 (J.H.C.), soldiers, workers; Wandering, 2 miles NW. of, 2.ii.56 (J.H.C.), alates, soldiers, workers, nymphs; Watheroo, 2 miles S. of, 28.x.55 (J.H.C. and F.J.G.), soldiers, workers, nymphs; Williams, 9 miles SSE. of, 2.xi.53 (J.H.C.), soldiers, workers; Williams, 20 miles NW. of, 2.xi.53 (J.H.C.), soldiers, workers; Wubin, 42 miles NE. of, 19.x.55 (J.H.C. and F.J.G.), queen, soldiers, workers, nymphs; Wubin, 17 miles NE. of, 19.x.55 (J.H.C. and F.J.G.), workers; Wubin, 4 miles ENE. of, 19.x.55 (J.H.C. and F.J.G.), workers; Wurarga, 9 miles W. of, 21.x.55 (J.H.C. and F.J.G.), soldiers, workers; Wyening, 2 miles N. of, 13.iv.53 (J.H.C.), soldiers, workers.

(*c*) *Biology*

As stated above, the nest of *A. hillii* is found only in the nest of *C. acinaciformis*. Nicholls (1929) recorded it from a mound of *C. lacteus* (Froggatt) but this species does not occur in Western Australia and Hill (1942) showed it to be a misidentification of *C. acinaciformis* or *C. raffrayi*. Hill stated that *A. hillii* is found in nests of "*Coptotermes*—probably *C. acinaciformis* or *C. raffrayi*". These forms are, however, only subspecifically distinct (Calaby and Gay 1956).

Before describing the nest and habits of *A. hillii* and *A. pumilus*, it is necessary to give a brief description of the nest of the host species (see Calaby and Gay (1956) for a more detailed description). When the *C. acinaciformis* nest takes the form of a domed mound it consists of three separate sections sharply demarcated from each other (see Fig. 2): (i) a hard outer clay wall up to about 2 ft in thickness, containing few galleries; (ii) a zone 3-6 in. thick (referred to hereafter as the "inner section") 2 ft or so in diameter, composed of fairly loose, flattish lumps of woody, honeycomb-like carton, which completely encloses; (iii) a roughly spherical nursery composed of concentrically arranged, thin, perforated lamellae of fragile, cardboard-like carton. Both the inner section and the nursery are thickly populated by the host insect.

In tree or stump colonies the inner section and nursery are as described above, but their shape may be modified by the wood or roots of the tree. The uneaten portion of the tree trunk may serve as the outer wall, though its base will often be built around with clay. The eaten-out centre of the tree, above nest level, is generally packed with damp clayey material. The nursery may be at ground level in tree colonies or a foot or more below ground level in tree or mound colonies.

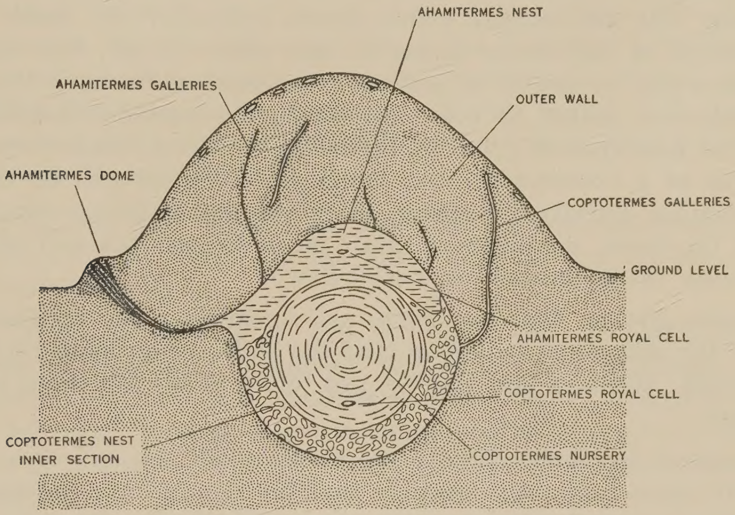

Fig. 2.—Cross section of mound of *Coptotermes acinaciformis* parasitized by a colony of *Ahamitermes hillii.*

The nest of *A. hillii* is always found directly above the nursery, occupying part of the inner section of the host's nest and often extending a few inches into the outer wall. Large, well-established *A. hillii* colonies occupy a large part of the inner section, but they never encroach on the nursery itself nor extend downward below the level of the centre of the nursery. The nest is composed of a mass of flattish, mostly horizontal, galleries or cells. Its dark, sooty-brown colour and architecture are very different from the yellow-brown lumps of carton of the *Coptotermes* nest.

A few *Ahamitermes* galleries, with characteristic dark-brown lining, traverse the clay outer wall of the host nest and sometimes the clay filling above the nest in tree colonies. There are also occasional small concentrations of *Ahamitermes* cells in the outer wall of the *Coptotermes* nest. The host insect is completely displaced from that portion of its nest invaded by *A. hillii.* The sketch in Figure 2 shows a cross section of a *C. acinaciformis* mound parasitized by an *A. hillii* colony. Plate 1, Figure 1, is a photograph of a partly dissected mound of *C. acinaciformis* containing a colony of *A. hillii,* the dark-coloured nest of which can be seen *in situ* above the spherical nursery.

The parasitic species maintains a connection with the outside world, usually by the construction of small domes outside the host's nest. The domes are up to 6 in. high and the same in base diameter, but are usually only 3 or 4 in. in diameter and about 2 in. high. They may be on the side or even the summit of the *Coptotermes* mound but are generally at, or a few inches from, the base of the mound or tree. One or two such domes are usual for each nest but up to seven have been found. The domes are largely composed of earthy material and are dark brown to black in colour, contrasting with the usually yellow-brown colour of the host's mound. Rehabilitation of the domes seems to take place rarely; they are often somewhat eroded or partly or completely covered with clay washed from the *Coptotermes* mound, or even covered during mound-enlarging operations by the host species. Plate 1, Figure 2, shows an *Ahamitermes* dome on the side of a *Coptotermes* nest which has been covered by the host's mound-building activity. A group of broad flat galleries occupies the centre of the dome, coming to within ½ in. of the surface and connecting directly with the *Ahamitermes* nest below.

It seems obvious that the domes are constructed for facilitating the escape of the alates and it is here that the alates congregate when ready for dispersal. Workers and soldiers are found in the domes at any time of the year.

Sometimes no domes have been found in an *Ahamitermes*-infested mound. In these cases it is possible that the domes have escaped notice through being engulfed by the host's mound-building activities. In one instance an *Ahamitermes* dome was found to have been overlain by the edge of a mound of *Amitermes obeuntis* Silvestri built against a *Coptotermes*-infested tree.

Two cases have been observed in which the connection by *A. hillii* with the outer world was apparently being maintained without the existence, or need, of the usual dome structures. The first was a *Coptotermes* mound in which the *Ahamitermes* galleries came to the surface in many places, and were covered at the emergence points with black earthy material. In the second—that of a nest built behind the wooden retaining wall under the end of a bridge—several *Ahamitermes* galleries came out between the timbers, continuing downwards over their surface for a few inches.

All observations lead to the conclusion that the sole food of *A. hillii* is the carton of the inner section of the *Coptotermes* nest, where the parasite's nest is located. Careful dissection of many nests has failed to reveal *Ahamitermes* workers eating wood or materials other than carton, even when the host's nest is built inside a tree. Many observations have been made of *Ahamitermes* eating the lumps of carton. The lumps are completely hollowed out and, when the resulting shells are broken open, considerable numbers of *A. hillii* workers are found inside.

From observations on dissected nests it appears that the sequence of invasion is probably as follows: the host is somehow dispossessed of a part of the inner section of its nest and a barrier is erected to exclude it. The *Ahamitermes* workers eat galleries through the carton, reducing the lumps to thin shells. Further galleries are eaten through the carton and it is bridged over with clay and faecal matter, transforming the loose lumps of *Coptotermes* carton to the dark-coloured, rigid, characteristic nest of the parasitic species. That *A. hillii* takes possession of the carton before eating through it is shown from observations that the carton lumps close to the *Ahamitermes* side of the boundary between the two species are most often not eaten into and retain their original appearance except that they are darker than the adjacent carton still occupied by *Coptotermes*, having been covered with a thin layer of what is undoubtedly *Ahamitermes* faecal material.

The soldiers and workers of both host and parasite are intolerant of all castes of the other species and attack them when the communal nest is broken open.

The king and queen of *A. hillii* are found near the centre of the nest in a large flat cell with somewhat thickened walls. The eggs and very small nymphs are located in separate groups of galleries close to the royal cell but separate from it. Supplementary reproductives have been found on only one occasion when two brachypterous neoteinics were collected from one nest.

Alates have been taken from nests in February, March, and April, and have been observed flying on one occasion only, on April 6, 1955. They came to a lamp at dusk and after dark, the first at 6.35 p.m., the last at 8.10 p.m., and they were flying in large numbers from 6.40 to 6.55 p.m. It was a warm sultry day with an overcast sky. A heavy shower of rain began at 5.40 p.m. and continued until 7 p.m., and there were intermittent showers during the night. Alates of *A. hillii* therefore disperse at a different season of the year to those of the host *C. acinaciformis*, the alates of which fly from October to early January but mostly in November (Calaby and Gay 1956).

IV. A. INCLUSUS

(*a*) *General*

A. inclusus is known from seven series, two of which are recorded by Gay (1955*a*) who also gives a brief description of a nest. Its host is *Coptotermes brunneus* Gay, and both host and parasite are apparently restricted in distribution to a limited area between the Murchison River and Shark Bay in sub-coastal Western Australia. *A. inclusus* is probably fairly common where it occurs, for the seven series were taken from only 27 *C. brunneus* nests examined, most of them superficially.

(*b*) *Distribution Records*

New records of *A. inclusus* are as follows: Five series from 43, 53, 62, 68, and 81 miles NNW. of Galena. All collected by J.H.C. and F.J.G., the first on 23.x.55 and the others on 24.x.55. All series contained soldiers, workers, and nymphs, except the second which was without nymphs.

(*c*) *Biology*

C. brunneus is a mound-building species and does not nest in trees. The mound, which differs somewhat in details of construction from that of *C. acinaciformis,* consists of a clay cone or dome up to 9 ft high and 5 ft in diameter, 3 ft above ground level. That portion corresponding to the inner section of a *C. acinaciformis* nest is generally almost entirely underground, and consists of a large, roughly ovoid mass of loose carton lumps. The nursery in the *C. brunneus* nest is well underground and differs considerably in construction from that of *C. acinaciformis.* The carton section of the nest is thickly populated with termites.

The nest of *A. inclusus* is in an analogous position in the *C. brunneus* nest to the nest of *A. hillii* in the *C. acinaciformis* nest, i.e. in the uppermost portion of the carton section. However, it is not in contact with the nursery. It is roughly spherical or irregular in shape and about a foot in diameter and is constructed similarly to *A. hillii* nests and has the same appearance. Galleries extend from the nest out into the walls of the *Coptotermes* mound, sometimes almost to the summit, and usually some run close to the surface. Only one of the seven colonies examined had built a dome which was at the base of the host's mound, and was similar in size, construction, and appearance to the domes of *A. hillii.*

As in the case of *A. hillii* the sole food of *A. inclusus* appears to be the carton material of the *Coptotermes* nest where the parasite's nest is situated. No evidence could be found of the *Ahamitermes* eating wood or materials other than *Coptotermes* carton.

The queen was found in a large flat cell at about the centre of one nest, and the eggs and very small nymphs in groups of nearby galleries separate from each other and from the queen. No neoteinic reproductives have been found.

The alate of *A. inclusus* is not known but it can be inferred from the size of reproductive nymphs found in October that the alates would fly in autumn. Thus the alates, like those of *A. hillii,* disperse at a different season of the year from those of its host which are ready to leave the nests in October. The soldiers and workers of both species are intolerant of all castes of the other.

V. A. PUMILUS

(*a*) *General*

A. pumilus is known from five series from widely separated localities, two in New South Wales and three from inland Western Australia

(Gay 1956). Although its distribution is the widest known of any species in the genus, it appears to be very rare. The nests from which the three Western Australian series were taken were examined in detail. Brief biological notes on this species are given by Hill (1942) and Gay (1956).

(*b*) *Biology*

A. pumilus is the most specialized member of the genus. It parasitizes *C. acinaciformis*, and the four series taken from nests were all from colonies of the host in living eucalypt trees. The nest of *A. pumilus* is found only in the nursery of the host's nest, and a careful search failed to reveal galleries of the parasite in any other part of the nest or outside of it. The *A. pumilus* colonies in the three nests examined were situated towards the lower side of the nursery and occupied about one-third to one-half of the nursery volume, and included the parts where the host's eggs and very small nymphs are normally located. The nest ends abruptly at the nursery boundary.

A. pumilus is a very small species and its workers eat out the thin perforated lamellae of which the host's nursery is composed, and this is without doubt its sole food. The lamellae are reduced to very thin shells, the interior of which are covered with a dark-coloured lining.

In the nests examined, the non-reproductive and immature castes of the parasite were entirely separated from the host insects, within their thin-walled flat galleries. The alates of *A. pumilus* are found in the nests in October and November, i.e. at the same time as those of its host. The mature alates must get from their own nest into the host's galleries and ascend up into the host's escape galleries in company with the *Coptotermes* alates. The parasite's alates are presumably released by the host's workers and disperse with the alates of the host. In two of the parasitized *Coptotermes* nests examined, the main escape galleries were, respectively, a clay-covered piped branch 12 ft from the ground and a clay-covered eaten-out branch stub about 4½ ft from the ground. Part of the clay covering from each was removed by a single sharp blow from an axe. The action was so rapid that it was possible to observe momentarily the dense mass of resting alates before they had time to move, and occasional *A. pumilus* alates were seen among the *Coptotermes* alates. It was also observed that when the communal nests were broken open the workers and soldiers of *A. pumilus* attacked all castes of *C. acinaciformis*, but, while the workers and soldiers of *C. acinaciformis* attacked the non-reproductive castes of the *Ahamitermes*, it appeared to the author and his colleagues (Messrs. F. J. Gay and D. L. McIntosh) who were present, that they ignored at least the great majority of the alates.

A brachypterous neoteinic is known from one colony of *A. pumilus* and an apterous neoteinic from another. Alates have been observed flying on one occasion only (by Mr. E. F. Riek), at Mt. Arthur, near Wellington, N.S.W., on November 26, 1949. The alates, together with alates of *C. acinaciformis,* were attracted to a lamp sometime between darkness (7 p.m.) and 11 p.m. The weather was warm and sultry and it had rained the previous day.

In view of the foregoing data on the biology of *A. pumilus,* it is interesting to note that the type series of workers, two soldiers, nymphs, and a brachypterous neoteinic is recorded (Hill 1942) as having been found in the nursery and other galleries of a populous colony of *C. acinaciformis.* Ratcliffe, Gay, and Greaves (1952) elaborate on this brief note and state that "there was no attempt at segregation on the part of the *Ahamitermes,* groups of workers, soldiers, and nymphs being found here and there in the very centre of the nest, mingling freely with the host species". The above authors' descriptions are very different to the present author's observations and are probably explained by the history of the series in question. The *Coptotermes* nursery containing the type series of *A. pumilus* was collected by Mr. F. N. Ratcliffe at Mt. Lindesay (N.S.W.), and sealed in a container and transported to the C.S.I.R.O. Division of Entomology at Canberra. The *A. pumilus* were found only after the package was opened at Canberra a couple of days or so later. It seems probable that, in the interval between the initial disturbance of the nursery and its examination in Canberra, the presumed hostilities between the species had subsided because of their acquisition of a common odour, and they had become mutually tolerant.

VI. Discussion

In the literature one finds many examples of the close association of two or more different species of termites, often contained in as many genera. The overwhelming majority of such associations are purely fortuitous. Different species may be under the same log because it is the common food supply or shelter, but their galleries are always clearly separated and they are hostile to one another when accidentally thrown together. The galleries of species inhabiting mounds built by others are most often restricted to the outer walls; but the species are not in contact and it is probable that when termites of one species or colony run into the galleries of another while tunnelling the breach would be quickly sealed off.

The author has several records of galleries of other species being tunnelled into the domes of *A. hillii.* The species involved in addition to the host, *C. acinaciformis,* were *Heterotermes ferox* (Froggatt), *Termes kraepelinii* (Silvestri), *T. iridipennis* Gay, two undescribed species of *Termes, Amitermes modicus* Hill, *A. obeuntis* Silvestri, and *Microcerotermes serratus* (Froggatt). There are many examples of different termite species inhabiting mound-builders' galleries but, in at least the great majority of these cases, the colonies are separate and sealed off from one another.

It is suggested that the frequency with which foreign termites are found occupying the walls and other parts of nests of mound-building species is due largely to the fact that the mounds are very solid and often the most durable and conspicuous earthy structures in the habitat. The mounds would therefore offer most favourable conditions for colony-founding and survival to those alates fortunate enough to alight and pair on them. It is also possible that flying alates are guided to mounds by visual stimuli.

The associations of species of the genera *Microtermes* and *Ancistrotermes*, belonging to the African and Oriental subfamily Macrotermitinae, have received a good deal of attention (see, for example, Hegh (1922) and Grassé (1944)). The nests of species of these genera are most commonly associated with mounds and other types of nests of species of other termitid genera. In the majority of cases at least, the associations are not species-specific and the nature of the relationship is unknown.

The only recorded termite nesting behaviour known to the author which resembles that of *Ahamitermes* is that displayed by the Neotropical *Termes inquilinus* (Emerson), which is found in, and utilizes as food a specific part of the nest of, *Constrictotermes cavifrons* (Holmgren) (Emerson 1938). The *Termes*, which is found only in the basal part of the *Constrictotermes* nest hanging from the underside of slanting trees, has never been found in any other situation and the relationship is species-specific. The basal part of the *Constrictotermes* nest is composed of a dark, pasty material which Emerson interprets as stored food. The colonies of host and parasite are separated and they display mutual intolerance when brought into contact. Emerson also mentions that the related *T. fur* (Silvestri) has a similar relationship with *Constrictotermes cyphergaster* (Silvestri).

Species of the genus *Termes* appear to nest in the walls of mounds of other species more frequently than could be attributed to chance, and is a common phenomenon in Australia. Skaife (1954) states that he has found colonies of the South African *T. winifredae* Snyder & Emerson only in the walls of mounds of *Amitermes atlanticus* Fuller. In practically all cases there is no contact between the *Termes* and the mound builder, but Hill (1942) gives data on one Australian species, *T. insitivus* (Hill), nymphs and alates of which have been found in the galleries of *Nasutitermes magnus* (Froggatt) intermingling with the host insects, and he cites some evidence that it may be a species-specific association. Unfortunately the non-reproductive castes of *T. insitivus* have not been found and nothing is known of the nature of the association.

The inner sections of the *Coptotermes* nest would certainly appear to provide ideal conditions for termites. They are extremely well sheltered, have a favourable microclimate, and have abundant food in the form of woody carton. It is not known whether the carton is utilized as food by the *Coptotermes*, but some of it is no doubt digested during nest-enlarging operations. It is of considerable interest that the various species of *Ahamitermes* are restricted in their nesting associations to either one of two species of *Coptotermes,* and apparently do not parasitize the four other species of this genus found in Australia. All of these species are well-known and a great many nests of two of them, *C. lacteus* (Froggatt) and *C. frenchi* Hill, have been examined in detail by C.S.I.R.O. entomologists. If either is parasitized by *Ahamitermes,* colonies would almost certainly have been found.

It appears certain that the *Ahamitermes* colony cannot persist in the absence of the host insect. Despite careful search no living *Ahamitermes* colony has ever been found in a nest deserted by *Coptotermes.* Three *C. acinaciformis–A. hillii* nests were observed which were deserted by both host and parasite, and one dying colony of the same species has been examined. The *C. acinaciformis,* which occupied a large mound of good external appearance, had apparently lost its original queen, for the only reproductive found was a functional apterous neoteinic female—an extremely rare occurrence (see Gay 1955*b*). There were very few live *Coptotermes* in the nest which was cold, wet, and mouldy, and there were masses of dead insects and many small white mites apparently feeding on their remains. The *A. hillii* colony was well populated and included reproductive nymphs, but it was cold and mouldy in the lower part and contained accumulations of dead termites.

There can be little doubt that the *Ahamitermes* colony does not prejudice the survival of the *Coptotermes* colony, or outgrow its food supply. *Ahamitermes* colonies are much smaller in size and population than are their hosts and it is probable that the growth of the host's nest more than makes up for the ravages of the parasite. Except for the case mentioned above, the large number of associated colonies found all appeared to be in a healthy state and most contained many alates or reproductive nymphs. One *Coptotermes* nest examined supported colonies of both *A. hillii* and *A. pumilus.* The *Coptotermes* and *A. pumilus* had many mature alates and the *A. hillii* many reproductive nymphs.

The selection of the nesting site by the *Ahamitermes* need not necessarily involve any special and complicated behaviour response, but the alates are possibly guided to the nests by visual stimuli. The hosts' nests are found in conspicuous mounds or trees, many of the mounds and trees being light in colour. They would thus reflect more light at night than surrounding objects. Alates of species of *Ahamitermes* are known to fly in the early hours of darkness, have large eyes, and are attracted to lights. The host is abundant and, in the case of *C. acinaciformis,* over large areas a high proportion of mature trees are infested by it.

The manner in which the original *Ahamitermes* pair establish themselves in populous parts of the nests of a much larger, numerous, and aggressive host is not known. Unfortunately, no incipient colonies of

Ahamitermes have yet been found. It is possible that the pair become established in the outer wall and migrate to their final location after raising a brood of workers and soldiers as suggested for other termite genera by Emerson (1938). Possibly the colony begins in the clay wall adjacent to the central carton section and expands from there, but it is emphasized that the royal cell of *Ahamitermes* is well inside the boundaries of this section. In view of the fact that alates of *A. pumilus* are released with those of their host, it is possible that they enter directly into the opened escape galleries of other colonies. However, this is considered unlikely as they would probably be destroyed by the soldiers. As there would be little more difficulty in getting into the nursery than into the inner section of the host's nest, the mode of entry is probably similar in all species of *Ahamitermes*. The alates of *A. pumilus* would no doubt have to be "conditioned" so that they would be accepted in the host's galleries.

The very specialized nesting behaviour of *Ahamitermes* presumably originated from a simple fortuitous association of the *Ahamitermes* ancestor with tree- or mound-nesting *Coptotermes*. A behaviour pattern has gradually evolved so that now each species of *Ahamitermes* is entirely dependent on either one of two species of *Coptotermes* for both food and shelter. The behaviour pattern has evolved still further with one species (*A. pumilus*) which is also completely dependent on the host for the release of its alates. It is noteworthy that this increasing trend of specialization of nesting behaviour is paralleled by increasing specialization of morphological characters of all castes. For example, the alate of *A. pumilus* is distinguished from its congeners by a further reduction of the already-reduced marginal teeth of the mandibles (an important character for phylogenetic studies (Ahmad 1950)), reduction of tibial spurs from 3:2:2 to 2:2:2, and other characters tending towards increasing specialization. It would seem that here we have an example of the beginning of generic separation.

VII. ACKNOWLEDGMENTS

The author is indebted to Mr. F. J. Gay for much helpful discussion, loan of reprints, and other favours; to Mr. L. A. Marshall for drawing the figures; and to Mr. D. L. McIntosh for technical assistance.

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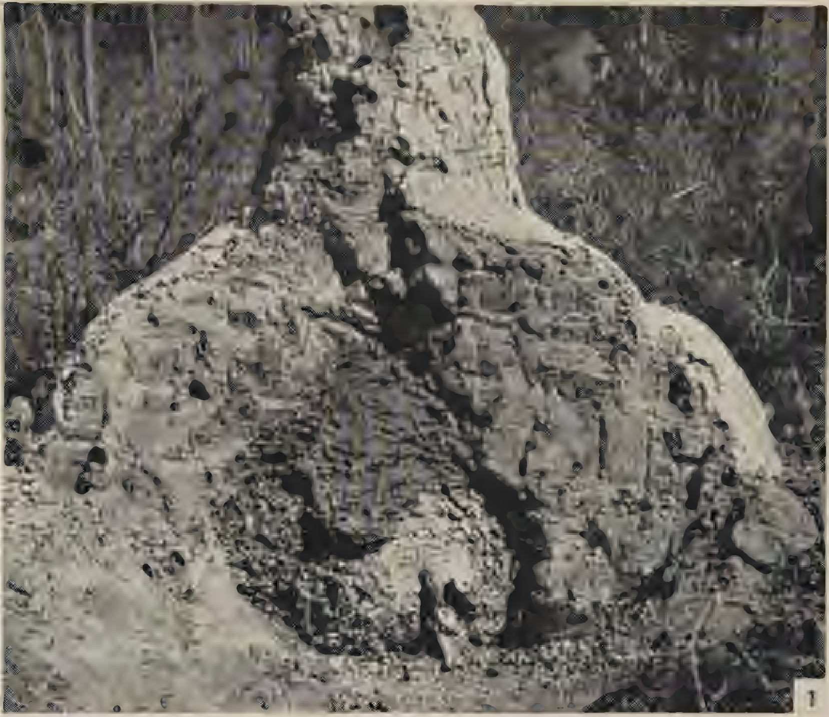
EXPLANATION OF PLATE 1

Photographs by J. H. Calaby

Fig. 1.—Photograph of partly-dissected mound nest of *C. acinaciformis* parasitized by a colony of *A. hillii.* The dark-coloured *Ahamitermes* nest can be seen above the *Coptotermes* nursery.

Fig. 2.—Photograph of mound nest of *C. acinaciformis* parasitized by a colony of *A. hillii.* The projection on the left-hand side of the mound towards the base is an *Ahamitermes* dome which has been completely covered by the host's mound-enlarging operations.

DISTRIBUTION AND BIOLOGY OF THE GENUS AHAMITERMES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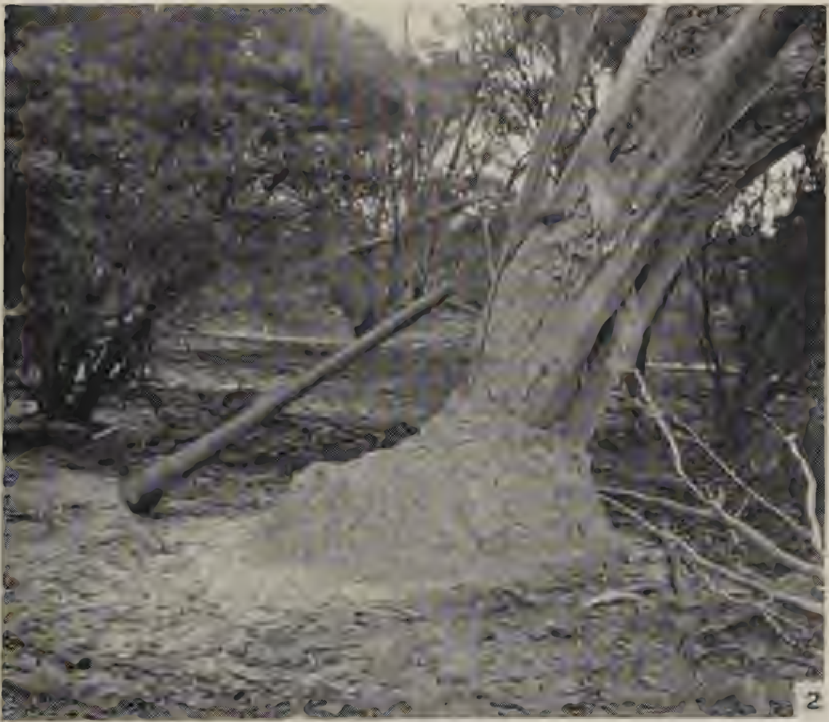
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THE EFFECT OF LIGHT ON THE FECUNDITY OF THE QUEENSLAND FRUIT-FLY, *STRUMETA TRYONI* (FROGG.)

By L. Barton Browne*

(*Manuscript received April* 27, 1956)

Summary

The number of eggs laid by *Strumeta tryoni* (Frogg.) was affected both by illuminance and by the daily period of illumination. Flies kept in constant darkness laid no eggs. When the daily period of illumination was 7½ hr, flies under 120 lm/sq. ft. laid fewer eggs than those under either 60 or 240 lm/sq. ft. At 60 and 240 lm/sq. ft. the flies laid approximately equal numbers of eggs. At an illuminance of 240 lm/sq. ft., the longer the daily period of illumination (up to 7½ hr) the greater was the number of eggs laid. Light had these effects on fecundity by influencing the amount of feeding, the rate of maturation of eggs, the readiness with which eggs were laid, and the age at which the flies mated. In constant darkness the flies fed very little, matured no eggs, laid few eggs even when gravid, and did not mate. When the daily period of illumination was 7½ hr, flies under an illuminance of 120 lm/sq. ft. fed less, matured eggs more slowly, and mated later in life than those under either 60 or 240 lm/sq. ft. The act of egg laying was not influenced by illuminance within the range 60-240 lm/sq. ft. When the illuminance was 240 lm/sq. ft., the longer the daily period of illumination (up to 7½ hr/day) the greater was the amount of feeding, the rate of maturation of eggs, and the number of eggs laid by mature females, and the earlier in life did the flies mate.

It is probable that the effects of light on feeding and egg laying were due to the influence that light had on the activity of the flies. They were inactive in darkness and were less active at 120 lm/sq. ft. than at either 60 or 240 lm/sq. ft. The effect of light on the rate of maturation of eggs can be explained by the effect of light on the amount of feeding.

I. Introduction

Myers (1952) showed that adults of *Strumeta tryoni* (Frogg.) kept in constant darkness did not mature eggs. He also showed that when groups of adults were kept under two illuminances, the group under the higher illuminance produced more larvae. These larvae were counted at rather a late stage of development and their numbers may not have given a good estimate of the numbers of eggs laid. The experiments described in this paper fall into two groups; those done to determine the effects of both illuminance and the length of the daily period of illumination on the number of eggs laid by *S. tryoni,* and those done to determine how light had its influence.

Light may have affected:

(*a*) The rate of maturation of eggs by influencing (i) the rate of secretion of a hormone necessary for the production of eggs, or (ii) the amount of food ingested.

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(*b*) Egg laying. Under certain illuminances and daily periods of illumination the flies may have retained mature eggs in their ovaries.

(*c*) The age at which the flies mated and the frequency of mating.

The second group of experiments was designed to determine what part these mechanisms played in producing the observed effects of light on fecundity.

II. Methods

(*a*) *Control of Temperature, Humidity, and Light*

All experiments and stock breeding were done in a warm room controlled at 26.6 ± 0.5°C. The thermoregulators were placed so that they received sufficient heat from the fluorescent tubes, used for lighting, to ensure that the temperature within the cages remained constant irrespective of whether the lights were on or off. The relative humidity was maintained at 75 ± 2 per cent. when the door of the warm room remained closed. When the door was opened frequently, fluctuations in relative humidity of up to 10 per cent. occurred. The air in the room was circulated by two electric fans.

All daylight was excluded from the room, except when the flies were exposed to natural dusk. Artificial illumination was supplied by two "Consolite 5000" fluorescent tubes mounted one above the other on the vertical wall at the back of each shelf on which the flies were kept. Mirrors were mounted vertically at the ends of the fluorescent tubes at right angles to them, so that the tubes and their images formed, in effect, infinitely long straight-line sources of light. All surfaces in the room had a matt black finish.

Since the flies mate only under dusk illumination (Myers 1952), they were exposed to natural dusk each day. The flies were placed in front of a window in the southern wall of the warm room 10 min before the official time of sunset and were allowed to remain there for 40 min. At the end of this time it was nearly dark and the flies, except those actually copulating, had ceased mating activity.

(*b*) *Breeding Methods*

Adult *S. tryoni* were kept in wire-framed organdie cages. They were provided with dry sucrose, a hydrolysate of yeast,* and cotton wool saturated with water. The cages were kept under an illuminance of 240 lm/sq. ft. for 7½ hr/day and under dusk illumination for about 40 min at the end of this period. All mating occurred during the dusk period. Flies for stock cultures were bred in papaws (*Carica papaya*). The flies laid their eggs directly into papaws which, when infested, were kept on an organdie platform so as to prevent the larvae from drowning in the fluid produced by the breakdown of the fruit. The number of eggs laid in a papaw was dependent on its ripeness. Apples gave much less variable results and were therefore used for oviposition when the number of eggs had to be counted. The flies used in all experiments described were bred in apples. Apples were artificially infested with eggs obtained from the stock culture at the rate of one egg to 4 g of apple tissue.

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* Manufactured by Marvin R. Thompson Inc., Stamford, Conn., U.S.A.

(*c*) *Techniques Used in Experiments*

Cages measuring 9 by 6 by 9 in. high were used in experiments. Each cage was of a colourless plastic ("Perspex") except for one 9 by 6 in. side which was fitted with a black organdie sleeve. The side opposite the sleeve faced the fluorescent tubes. The flies for each experiment were drawn randomly from large numbers of newly emerged flies which had been bred in apples and had passed their larval and pupal stages in constant darkness. The flies were transferred to clean cages every 2 weeks.

Unless otherwise stated, the flies were fed on the mixture used by Myers (1952) which consisted of: papaw paste 60 parts; banana paste 10 parts; orange paste 6 parts; and honey 1 part. This was given in 2-in. watch-glasses filled so that the surface available was always the same, and was renewed each day during the last ½ hr that the flies were under "day" illumination. Dry sucrose was supplied in 2-in. watch-glasses. Cotton wool saturated with water was given in 1½-in. diameter jars. The positions in the cages occupied by these different foods were constant.

The flies were exposed to illuminances of 240, 120, or 60 lm/sq. ft., as measured inside the cages at the end nearest to the fluorescent tubes. These illuminances were obtained 5 cm from two tubes, one tube, and a half tube (a tube painted so that only half its vertical height remained uncovered) respectively. Flies were exposed to three different daily periods of illumination: 2, 4, and 7½ hr. It was not practicable to work with a period of illumination of longer than 7½ hr. Five combinations of illuminance and daily periods were used. In a number of experiments all the combinations were used. To avoid repetition later these combinations are listed here:

60 lm/sq. ft. for 7½ hr
120 lm/sq. ft. for 7½ hr
240 lm/sq. ft. for 7½ hr
240 lm/sq. ft. for 4 hr
240 lm/sq. ft. for 2 hr

III. DESIGN OF EXPERIMENTS AND RESULTS

(*a*) *Fecundity and Pre-oviposition Period*

A group of five cages each containing eight males and eight females was exposed, from the time of emergence of the flies until the end of the 7th week of adult life, to each of the combinations of illuminance and daily period listed in Section II (*c*), and to natural dusk for 40 min at the end of the period of illumination each day. A further five cages were kept in darkness for 23⅓ hr/day and were exposed to light only during the 40-min dusk period. The numbers of eggs laid were counted as follows: Domes of apple skin, made by scooping the tissue from a small portion of apple so that about 1 mm thickness of flesh still adhered to the skin, were provided for oviposition. Forty holes were made in each dome with a fine pin. The eggs laid were counted on the inner surfaces of the domes. A fresh dome was placed in each cage each day. The apples from which the domes were made were of the same variety as those in which the flies had been bred. The percentage of eggs which hatched was determined by counting the number of unhatched eggs in the domes of apple skin after they had remained in a saturated atmosphere for the 24 hr following removal from the cages. The results are presented so as to show separately the effects of illuminance and daily period of illumination.

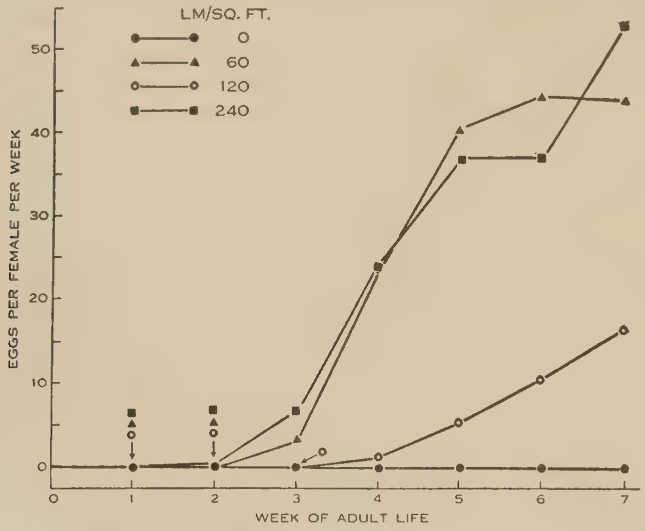

Fig. 1.—Effect of illuminance on the number of eggs laid per female per week (period of illumination 7½ hr per day). The effect of illuminance is significant ($P < 0.01$). The interaction between age and illuminance is also significant ($P < 0.01$). Means differing by 10 are significantly different at the 0.05 level.

(i) *Illuminance.*—Figure 1 and Table 1 show that illuminance affected fecundity. Flies kept in darkness except for the dusk period laid no eggs. When the daily period of illumination was 7½ hr, the flies under 120 lm/sq. ft. laid fewer eggs than those under either 60 or 240 lm/sq. ft. At 60 and 240 lm/sq. ft. the flies laid approximately equal numbers of eggs. Illuminance also affected the pre-oviposition period. The mean age at which flies under illuminance of 60, 120, and 240 lm/sq. ft. first laid eggs were 20.0, 31.8, and 15.8 days. Thus, exposure to 120 lm/sq. ft. stimulated egg production less effectively than lower (60 lm/sq. ft.) or higher (240 lm/sq. ft.) illuminances. Illuminance had no significant effect on the percentage of eggs which hatched—94.1 per cent., 94.7 per cent., and 92.3 per cent. hatched at 60, 120, and 240 lm/sq. ft.

TABLE 1

EFFECT OF LIGHT ON FECUNDITY

The number of eggs per female laid during the first 7 weeks of adult life. Effects of illuminance and daily period of illumination are significant at the 0.01 level

Illuminance (lm/sq.ft.)	Period of Illumination (hr/day)	No. of Eggs per Female to End of 7th Week of Adult Life	
		Mean	Coeff. of Variability (%)
Constant darkness*	Constant darkness*	0	—
60	7½	154.2†	26.2
120	7½	33.1	19.4
240	7½	156.7†	13.1
240	4	86.0	21.7
240	2	10.2	129.0

* Except for dusk period.

† Do not differ significantly at the 0.05 level.

(ii) *Daily Period of Illumination.*—Figure 2 and Table 1 show that, at an illuminance of 240 lm/sq. ft., the greater the number of hours of illumination each day the greater was the number of eggs laid. Furthermore, the longer the daily period of illumination at 240 lm/sq. ft., the

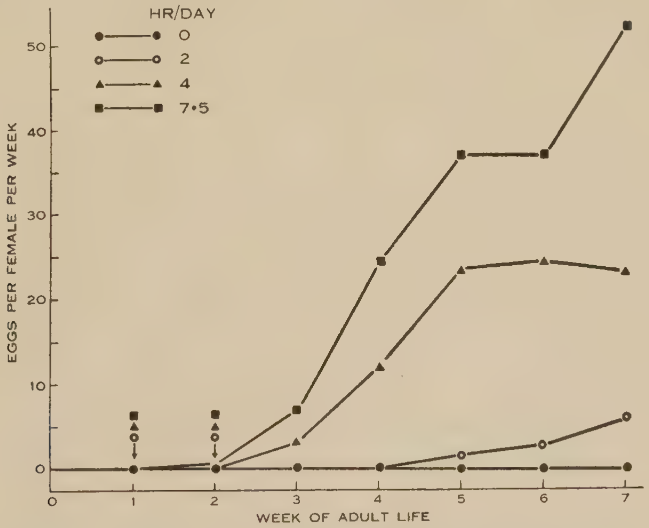

Fig. 2.—Effect of the daily period of illumination on the number of eggs laid per female per week (illuminance 240 lm/sq. ft.). The effect of daily period is significant ($P < 0.01$). The interaction between age and daily period is also significant ($P < 0.01$). Means differing by 8 are significantly different at the 0.05 level.

shorter was the pre-oviposition period. The mean age at which flies illuminated for 7½ hr/day commenced to lay was 15.8 days, and that for flies under 4 hr illumination per day was 19.6 days. In only four of the five cages illuminated for 2 hr/day had the flies laid eggs by the end of the 7th week. The daily period of illumination had no significant effect on the percentage of eggs which hatched—92.8 per cent., 91.0 per cent., and 92.3 per cent. emergences were recorded for daily periods of 2, 4, and 7½ hr respectively.

(*b*) *The Rate of Maturation of Eggs*

The effects of light on the rate of maturation of eggs was examined in both virgin and mated females.

Table 2

EFFECT OF LIGHT ON THE RATE OF MATURATION OF EGGS IN VIRGIN FEMALES

The effects of illuminance and daily period of illumination are significant at the 0.05 and the 0.01 levels respectively

Illuminance (lm/sq.ft.)	Period of Illumination (hr/day)	No. of Eggs per Female per Week	
		Mean	Coeff. of Variability (%)
Constant darkness	Constant darkness	0	—
60	7½	3.70*	23.4
120	7½	2.45†	13.6
240	7½	3.52*	15.7
240	4	2.53†	25.7
240	2	0.97	26.6

*† Do not differ significantly at the 0.05 level.

(i) *Virgin Females.*—A group of five cages each containing 12 virgin females was exposed, from the time of emergence of the flies, to the five combinations of illuminance and daily period listed in Section II(*c*) and to constant darkness. A further group of five cages containing flies whose eyes had been completely covered with black paint dissolved in benzol was exposed to 240 lm/sq. ft. for 7½ hr/day. At the end of 6 weeks the flies were dissected and the number of mature eggs in their ovaries counted.

Table 2 shows the results obtained. Illuminance affected the number of eggs in the ovaries of 6-week-old virgin females. The flies kept in constant darkness matured no eggs. When the daily period of illumination was 7½ hr the flies under 120 lm/sq. ft. matured fewer eggs than those under either 60 or 240 lm/sq. ft. At 60 and 240 lm/sq. ft. the flies matured eggs at approximately the same rate. At an illuminance of 240 lm/sq. ft., the greater the number of hours of illumination per day the greater was the rate of maturation of eggs.

The flies whose eyes were covered matured no eggs. This result was the same as that for flies in constant darkness. Controls whose eyes had been painted with benzol only, developed eggs normally. The rate of ovarian development was, therefore, probably dependent on the amount of light received by the eyes.

(ii) *Mated Females.*—Five cages each containing eight female flies were exposed, from the time of emergences of the flies, to 240 lm/sq. ft. for 7½ hr/day. A further five cages were exposed to 240 lm/sq. ft. for 2hr/day. Each day, eight sexually mature males were released into each of the 10 cages 1 hr before their exposure to natural dusk and were removed again after the dusk period. In this way the females were induced to copulate as soon as they were sexually active. The age of the flies when each copulation occurred was noted. The females were at no time provided with fruit for oviposition. When the females which had been illuminated for 2 hr/day were 6 weeks old, they were dissected under Drosophila saline (Ephrussi and Beadle 1936) and their spermathecae and ovaries examined. The number of eggs in the ovaries of fertilized flies were counted. The flies kept under illumination for 7½ hr/day were dissected when 4 weeks old because they began to lay eggs on the walls of the cages and in the moistened cotton wool.

TABLE 3

NUMBERS OF EGGS IN THE OVARIES OF MATED AND UNMATED FLIES

All means are significantly different at the 0.01 level

Period of Illumination (hr/day)	No. of Eggs per Mated Female in Ovaries at Age 4-6 Weeks (2 hr illumination) and 4 Weeks (7½ hr illumination)		No. of Eggs per Female in Ovaries of Virgins at Age of 6 Weeks	
	Mean	Coeff. of Variability (%)	Mean	Coeff. of Variability (%)
2	12.5	14.9	5.8	26.6
7½	34.1	14.9	21.1	15.7

Table 3 shows that mating increased the rate of maturation of eggs. An approximate estimate of the rate of maturation of eggs in mated females may be calculated from the results in this table, from the rates for virgin females, and from the mean age at which the flies in each cage mated. The mean rate at which eggs were matured was 3.7 eggs per female per week for mated females illuminated for 2 hr/day. That for flies illuminated for 7½ hr/day was 16.5 eggs per female per week. For mated flies illuminated for 7½ hr/day the mean rate at which eggs were developed was 4.46 times that for flies illuminated for 2 hr/day. For unmated flies this ratio was 3.64. Thus mating, although increasing the rates of development, only slightly altered the relative rates in flies under the two daily periods.

(*c*) *The Amount of Feeding*

The effect of light on the amount of feeding was investigated in three series of experiments. The first two series of experiments were done to determine the relation between light and the amount of feeding. The third series examines the interaction between type of food and the rate of maturation of eggs.

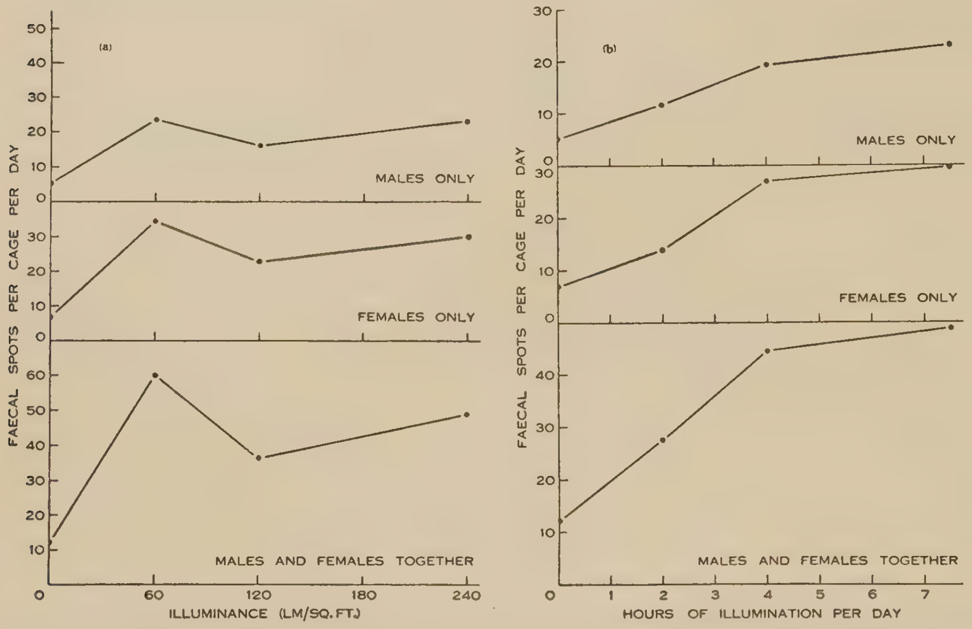

Fig. 3.—(*a*) Effect of illuminance on the number of faecal spots per day during the first 14 days of adult life (period of illumination $7\frac{1}{2}$ hr/day); and (*b*) effect of the daily period of illumination on the number of faecal spots per day during the first 14 days of adult life (illuminance 240 lm/sq. ft.). The effects of both illuminance and daily period of illumination are significant ($P < 0.01$). Males produce significantly ($P < 0.01$) fewer spots than did females. Means differing by 4 are significantly different at the 0.05 level.

(i) *Estimation of Feeding by Counts of Faecal Spots.*—Direct estimates of the amount of feeding could not be made on a food such as the papaw mixture since changes in weight due to evaporation and the action of microorganisms were large compared with the weight eaten. An indirect method, namely that of counting faecal spots, was therefore employed.

A group of five cages each containing eight females, a group each containing eight males, and a group containing eight males and eight females were exposed to each of the combinations of illuminance listed in Section II(*c*) and to constant darkness.

The faecal spots on each of the "Perspex" surfaces of the cages were counted at 2-day intervals during the first 14 days of adult life. Faecal spots on the dark organdie sleeve could not be counted. Their number was estimated from the distribution of spots when flies were kept in constant light and in constant darkness. Figures 3(*a*) and 3(*b*) show the effects of illuminance and daily period on the number of faecal spots produced. For each particular illuminance and daily period, the mean number of spots in cages containing eight males and eight females agreed closely with the total obtained when the mean number of spots in cages containing the sexes separately were added together. Flies in constant darkness produced fewer spots than those under any other conditions tested. When the daily period was 7½ hr, flies under an illuminance of 120 lm/sq. ft. produced less spots than those under either 60 or 240 lm/sq. ft. At 60 lm/sq. ft. the flies produced a slightly greater number of spots than at 240 lm/sq. ft. When the illuminance was 240 lm/sq. ft., the longer the daily period of illumination the greater was the number of faecal spots produced. Males produced fewer spots than did females.

TABLE 4

EFFECT OF ILLUMINANCE ON THE RELATIVE AMOUNTS OF FEEDING ON PAPAW MIXTURE, SUGAR, AND WATER

The effect of illuminance is not significant at the 0.05 level

Illuminance (lm/sq.ft.)	Percentage of Total Feeding on Papaw				Percentage of Total Feeding on Sugar				Percentage of Total Feeding on Water			
	Male		Female		Male		Female		Male		Female	
	Mean	Coeff. of Variability (%)	Mean	Coeff. of Variability (%)	Mean	Coeff. of Variability (%)	Mean	Coeff. of Variability (%)	Mean	Coeff. of Variability (%)	Mean	Coeff. of Variability (%)
60	61.0	16.2	72.0	16.0	13.0	28.2	16.6	30.9	26.0	27.2	11.4	65.8
120	58.9	18.9	62.3	20.6	22.4	34.6	17.3	31.2	18.7	53.5	20.4	72.5
240	65.1	21.0	69.5	18.6	16.2	25.2	12.8	19.7	18.7	49.2	17.7	46.3

(ii) *Direct Observations on Feeding.*—The only source of protein was the papaw mixture and the amount of this food eaten would presumably play the major part in controlling egg production. Before the numbers of faecal spots produced could be used as reliable measures of the relative amounts of protein eaten, it was necessary to know whether the relative amounts of papaw mixture, sugar, and water ingested were the same for flies under each illuminance.

A group of five cages each containing eight males and eight females were exposed, from the time of emergence of the flies, to each of illuminances of 60, 120, and 240 lm/sq. ft. for 7½ hr/day. The number of flies of each sex feeding on papaw, on sugar, and on water was counted at 1-min intervals throughout the light periods on the 3rd, 7th, and 12th days after emergence.

Table 4 shows that the relative amounts of feeding on each were similar for each illuminance. The counts of faecal spots could therefore be used as an indication of the relative amounts of protein eaten by the flies under different illuminances and daily periods. Table 5 confirms the results obtained by counting faecal spots. The total number of flies feeding under an illuminance of 120 lm/sq. ft. was less than under either 60 or 240 lm/sq. ft. Figure 4 shows that the flies under each illuminance fed most frequently during the first hour after the lights were switched on. This probably accounted for the comparatively small difference between the numbers of faecal spots deposited by flies illuminated for 2, 4, and 7½ hr/day.

TABLE 5

EFFECT OF ILLUMINANCE ON THE TOTAL AMOUNT OF FEEDING DURING THE LIGHT PERIODS ON 3RD, 7TH, AND 12TH DAYS OF ADULT LIFE

The effect of illuminance is significant at the 0.01 level. The amount of feeding by males is significantly (at the 0.01 level) less than that by females

Illuminance (lm/sq.ft.)	Total No. of Males Observed Feeding per Cage		Total No. of Females Observed Feeding per Cage	
	Mean	Coeff. of Variability (%)	Mean	Coeff. of Variability (%)
60	145.8*	22.4	184.0†	16.2
120	67.8	40.6	112.8	36.9
240	121.8*	21.9	180.4†	20.1

*† Do not differ significantly at the 0.05 level.

(iii) *Rate of Maturation of Eggs in Females Fed on Yeast Hydrolysate.*—The yeast hydrolysate contains 70 per cent. of protein as compared with less than 1 per cent. in the papaw mixture. If the rate of maturation of eggs under different illuminances and daily periods is limited by the amount of protein ingested then the effect of light on this rate would almost certainly be less marked in flies fed on protein hydrolysate than in those fed on the papaw mixture. Five cages each containing 16 virgin females were therefore kept from the time of emergence under 240 lm/sq. ft. for 7½ hr/day and were fed on yeast hydrolysate. A further five cages were kept in constant darkness. The females were dissected when they were 10 days old and the number of mature eggs in their ovaries counted. Flies kept in constant darkness matured eggs just as rapidly as those under illumination for 7½ hr/day, the mean rates being 24.9 and 25.7 eggs per female in 10 days, respectively. At least for flies fed on the yeast hydrolysate, light is not necessary for the maturation of eggs. It is probable, therefore, that the amount of feeding limited the rate of maturation of eggs in flies fed on the papaw mixture.

The first two series of experiments described in this section show that egg production and feeding are strongly correlated. The experiments with females fed on the yeast hydrolysate show that light is not necessary for egg production provided sufficient protein is eaten. Both these findings indicate that the effect of light on the rate of maturation of eggs is a direct one, i.e. the number of eggs matured is dependent on the amount of protein eaten. The relationship, however, cannot be a simple one since mating increases the rate of maturation of eggs. The utilization of protein in mated females must therefore be different from that in virgins. The possibility that food may have influenced the production of a gonadotrophic hormone has not, however, been ruled out by these experiments.

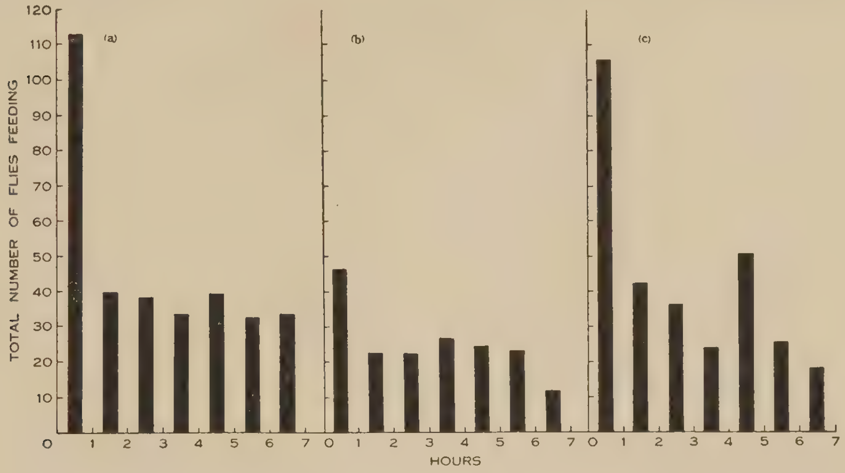

Fig. 4.—Number of flies feeding each hour during the day periods on days 3, 7, and 12 of adult life. (*a*) 60 lm/sq. ft.; (*b*) 120 lm/sq. ft.; (*c*) 240 lm/sq. ft.

(*d*) *Egg Laying*

When flies were exposed to an illuminance of 240 lm/sq. ft. for $7\frac{1}{2}$ hr/day they laid 97 per cent. of their eggs during the light period. Thus, as well as affecting the rate of maturation of eggs, light may have influenced the rate at which they were laid. Under certain illuminances and daily periods flies may have retained mature eggs in their ovaries.

(i) *The Number of Eggs Laid under Different Illuminances and Daily Periods.*—Flies were kept from the time of their emergence under an illuminance of 240 lm/sq. ft. for $7\frac{1}{2}$ hr/day and were given the opportunity to mate and oviposit every day. When these flies were 5 weeks old, six groups of five cages, each containing eight females, were set up. Each of these groups was exposed for 24 hr to one of the combinations of illuminance and daily period listed in Section II (*c*) and to constant darkness, and the number of eggs counted.

Table 6 shows the results obtained. When the daily period was $7\frac{1}{2}$ hr, the numbers of eggs laid by flies under illuminances of 60, 120, and 240 lm/sq. ft. did not differ significantly. The period of illumination affected the number of eggs laid. Under 240 lm/sq. ft. the longer the period of illumination the greater was the number of eggs laid. Flies in darkness for 24 hr laid fewest eggs of all. These results suggest that flies kept throughout their adult lives under an illumination of 240 lm/sq. ft. for 4 or 2 hr/day may not have been able to lay all the eggs that they had matured.

Table 6

EFFECT OF LIGHT ON THE ACT OF EGG LAYING

The number of eggs laid when flies were exposed to different illuminances and daily periods of illumination are given. The effects of illuminance and daily period of illumination are significant at the 0.01 level

Illuminance (lm/sq.ft.)	Period of Illumination (hr/day)	No. of Eggs Laid per Female per Day	
		Mean	Coeff. of Variability (%)
Constant darkness	Constant darkness	0.39	41.0
60	7½	5.40*	12.1
120	7½	4.88*	14.1
240	7½	5.62*	10.5
240	4	4.60*	12.1
240	2	3.42	12.0

* Do not differ significantly at the 0.05 level.

(ii) *The Number of Eggs Retained in the Ovaries of 7-Week-Old Flies.*—Five cages each containing eight males and eight females were kept from the time of emergence under each of the combinations of illuminance and daily period listed in Section II (*c*). The flies were given the opportunity to mate and oviposit every day. After 7 weeks the females were dissected and the number of eggs in the ovaries of mated females was counted.

Table 7

EFFECT OF LIGHT ON THE NUMBER OF EGGS RETAINED IN THE OVARIES OF FLIES WHICH HAD BEEN GIVEN THE OPPORTUNITY TO OVIPOSIT FOR THE 7 WEEKS FOLLOWING EMERGENCE

The effect of illuminance is not significant at the 0.05 level, the effect of daily period of illumination is significant at the 0.01 level

Illuminance (lm/sq.ft.)	Period of Illumination (hr/day)	No. of Eggs per Female	
		Mean	Coeff. of Variability (%)
Constant darkness	Constant darkness	0	—
60	7½	8.2*	43.9
120	7½	7.0*	41.4
240	7½	7.4*	52.7
240	4	9.8*	36.8
240	2	19.6	15.2

* Do not differ significantly at the 0.05 level.

The results obtained are shown in Table 7. The number of eggs retained by flies kept under any of the three illuminances for 7½ hr/day did not differ significantly. Flies which had been kept under 240 lm/sq. ft. for 2 hr/day retained more eggs in their ovaries than those kept under this illuminance for either 4 or 7½ hr/day. This was despite the relatively slow rate of maturation of eggs in flies illuminated for 2 hr/day. The number of eggs in the ovaries of flies kept under illumination for 4 hr/day was slightly, but not significantly, higher than in flies kept under illumination for 7½ hr/day.

(*e*) *Mating*

Experiments were designed to determine the effects of light on the age at which the flies mated and on the frequency of mating and to determine the effects of mating on the rates of maturation and laying of eggs.

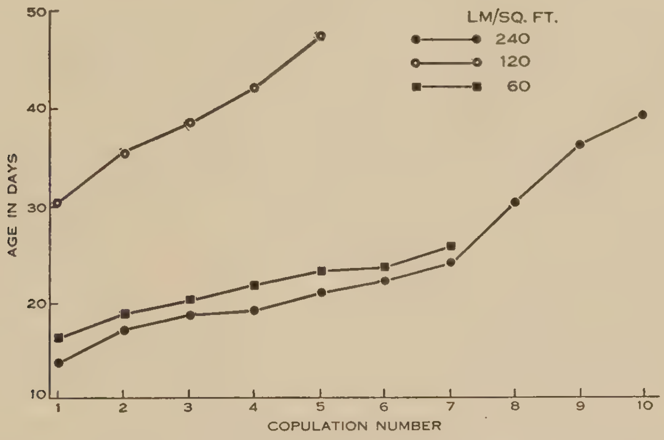

Fig. 5.—Ages of flies when each copulation occurred in cages containing eight males and eight females kept under different illuminances for 7½ hr per day. The effect of illuminance is significant ($P < 0.01$). Means whose logarithms differ by 0.0980 are significantly different at the 0.05 level.

(i) *The Ages of the Flies when Mating Occurred and the Frequency of Mating under Different Illuminances and Daily Periods of Illumination.*—A group of five cages each containing eight males and eight females was exposed from the time of emergence of the flies to the combinations of illuminance and daily period listed in Section II (*c*) and to natural dusk for 40 min at the end of the period of illumination each day. A further group of five cages was kept in darkness for 23⅓ hr/day and was exposed to the light only during the 40-min dusk period. The number of copulations occurring each day was counted. This could be done since flies copulated only during the 40 min of dusk each day.

Figure 5 and Table 8 shows that the age of the flies when each copulation occurred and the frequency of copulation during the first 7 weeks of adult life were affected by illuminance. Flies in darkness for $23\frac{1}{3}$ hr did not mate. When the daily period of illumination was $7\frac{1}{2}$ hr the flies under 120 lm/sq. ft. mated later in life and less frequently than those under either 60 or 240 lm/sq. ft. At 60 and 240 lm/sq. ft. the ages of the flies when the copulations occurred and the frequencies of copulation

TABLE 8

EFFECT OF LIGHT ON THE FREQUENCY OF MATING

The number of copulations per female to the end of the 7th week of adult life are given. The effects of both illuminance and daily period of illumination differ significantly at the 0.01 level

Illuminance (lm/sq.ft.)	Period of Illumination (hr/day)	Number of Copulations per Female to the End of the 7th Week	
		Mean	Coeff. of Variability (%)
Constant darkness	Constant darkness	0	—
60	$7\frac{1}{2}$	1.41*	16.3
120	$7\frac{1}{2}$	0.62†	17.7
240	$7\frac{1}{2}$	1.46*	13.6
240	4	1.03	16.5
240	2	0.68†	63.2

*† Do not differ significantly at the 0.05 level.

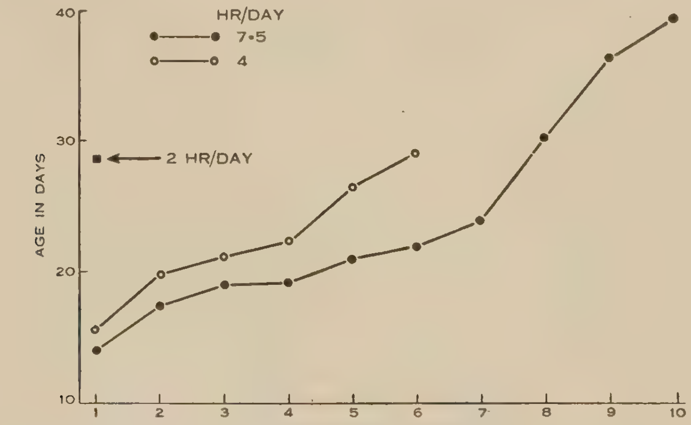

Fig. 6.—Ages of flies when each copulation occurred in cages containing eight males and eight females kept under an illuminance of 240 lm/sq. ft. for different daily periods of illumination. The effect of daily period of illumination is significant ($P < 0.01$). Means whose logarithms differ by 0.1015 are significantly different at the 0.05 level.

were approximately the same. Figure 6 and Table 8 show that under 240 lm/sq. ft. the longer the daily period of illumination the greater was the frequency of copulation and the younger were the flies at copulation.

(ii) *The Number of Females that Participated in the First Eight Copulations in a Cage Containing Eight Females.*—Five cages each containing eight males and eight females were kept under an illuminance of 240 lm/sq. ft. for 7½ hr/day, followed each day by exposure for 40 min to natural dusk. After eight copulations had occurred in a cage the females in it were dissected and their spermathecae examined for the presence of sperm. The mean number of females per cage whose spermathecae contained sperm was 7.4. The mean ages when the first eight copulations occurred (Figs. 5 and 6) therefore give an indication of the mean ages at which each of the first eight females in a cage mated.

TABLE 9

EFFECT OF MATING ON THE RATE OF MATURATION OF EGGS

The numbers of eggs matured per female per week when flies were mated and unmated are given. The means for mated and unmated females are significantly different at the 0.01 level

Illuminance (lm/sq.ft.)	Period of Illumination (hr/day)	No. of Eggs per Week			
		Mated		Unmated	
		Mean	Coeff. of Variability (%)	Mean	Coeff. of Variability (%)
240	2	3.7	14.9	0.97	26.6
240	7½	16.5	14.9	3.52	15.7

(iii) *The Effect of Mating on the Rate of Maturation of Eggs.*—Experiments were described previously in this paper in which the rates of maturation of eggs were determined for mated and unmated females. Table 9 shows that mating increased the rate of maturation of eggs in flies kept under an illuminance of 240 lm/sq. ft. for 2 and for 7½ hr/day. In each case the mated flies matured eggs about four times as rapidly as the unmated ones.

The effect of mating on the rate of maturation of eggs has been little studied in insects. The rate is unaffected by mating in *Rhagoletis completa* Cresson (Boyce 1934). *Anopheles punctulatus* Dönitz (Roberts and O'Sullivan 1948), *A. stephensi* Liston and *A. annulatus* van der Wulp (Roy 1940), and *A. algeriensis* Theo. (Bates 1949, p. 89) have been shown to mature eggs when unmated, but the rates for mated and unmated females were not compared. Like *S. tryoni, Locusta migratoria migratoriodes* (Reiche & Fairm.) develops eggs when unmated but develops them more rapidly when mated (Phipps 1950). *Anopheles subpictus* Grassi

(Roy 1940), *A. superpictus* Grassi, and most of the *A. maculipennis* Meig. group (Bates 1949, p. 89) do not mature eggs when unmated.

(iv) *The Effect of Mating on Oviposition.*—The flies were fed on protein hydrolysate. Five cages each containing eight virgin females were kept from the time of their emergence for 6 weeks under an illuminance of 240 lm/sq. ft. for 7½ hr/day. They were exposed to dusk for 40 min each day at the end of the period of illumination. A second group of five cages each containing eight males and eight females was treated similarly. In these cages the females had mated by the end of the 4th week. The number of eggs laid was counted each day and the number retained in the ovaries was counted at the end of 6 weeks. Figure 7 shows that mated females laid more eggs than unmated ones. The mean number of eggs retained in the ovaries of unmated females was 51.2 eggs per female and that in mated females only 20.1 eggs per female. Mating clearly stimulated the flies to lay eggs they had already matured. A similar result has been shown for *Anopheles punctulatus* which if unmated will retain a single batch of eggs throughout life (Roberts and O'Sullivan 1948).

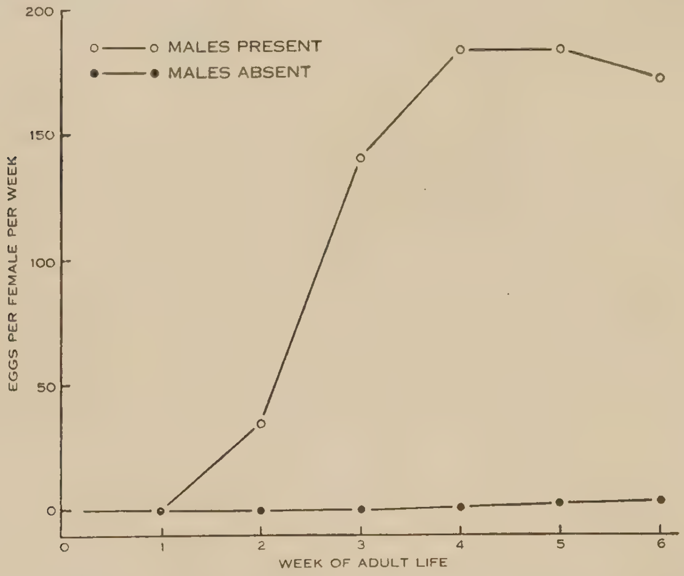

Fig. 7.—Effect of mating on the number of eggs laid. The number of eggs laid per female when females were kept alone and when males and females were kept together is shown. The effect of mating is significant ($P < 0.01$).

The fecundity of a number of insects has been shown to be increased by mating. These include *Tribolium confusum* Duval (Park 1933), *Laemophloeus minutus* Oliv. (Davies 1949), *Tribolium destructor* Uylt. (Reynolds 1944), and *Drosophila melanogaster* Meig. (Hanson and Ferris 1929). It is not known, however, whether mating affected the rate of maturation of eggs, or stimulated the insect to lay, or both.

The experiments described in this section show that the ages at which the flies mated and the frequencies of mating were different when flies were kept under different illuminances and daily periods. Mating affects both the maturation and laying of eggs. One of the ways in which light affects fecundity is therefore by affecting the mating of the flies.

IV. DISCUSSION

The results are discussed from two points of view:

(*a*) The effects of (i) illuminance and (ii) daily period of illumination on the maturation of eggs, feeding, and egg laying are examined. The effect of light on mating will be dealt with in a later paper.

(*b*) The fecundity rates of the flies under each illuminance and daily period are discussed by referring to the rate of maturation of eggs, the rate at which the already mature eggs were laid, and the age at which the flies mated.

(*a*) *The Effect of Light on the Rate of Maturation of Eggs, on Feeding, and on Egg Laying*

(i) *Illuminance* (*daily period* 7½ *hr*).—Flies in constant darkness matured no eggs, fed little, and did not mate. Flies under 120 lm/sq. ft. matured eggs less rapidly and fed less than those under either 60 or 240 lm/sq. ft. The act of egg laying was little affected by illuminance within the range of 60-240 lm/sq. ft.; darkness almost completely inhibited egg laying.

Although the level of general (as distinct from sexual) activity of the flies under different illuminances was not measured quantitatively, flies under 60 and 240 lm/sq. ft. were noticeably more active than those under 120 lm/sq. ft. Flies in darkness were still less active than those under 120 lm/sq. ft. It was probably through its effect on general activity that light influenced feeding, maturation of eggs, and egg laying. When flies moved freqently the chance of their alighting on food was greater than if they moved less frequently. It is possible also that more active flies were more readily attracted by the odour of food. The rate of maturation of eggs was influenced by the amount of feeding. Since egg laying was inhibited by darkness, the general activity of flies may also have influenced the act of egg laying.

Insects which are inactive in darkness might be expected to be more active under high illuminances than under low ones. Above 120 lm/sq. ft. the expected increase in activity with increasing illuminance occurred. The high general activity of flies under 60 lm/sq. ft. may perhaps be explained as follows: When flies were exposed to low illuminances (dusk) they became sexually active. Their general activity was then much greater than at high illuminances. When flies were exposed to natural light about half an hour before sunset they showed increased general activity at illuminances considerably above those at which they became sexually active. An illuminance of 60 lm/sq. ft. was apparently sufficiently close to a dusk illuminance to cause the flies to show greater general activity than did those under an illuminance of 120 lm/sq. ft. (see Fig. 8).

(ii) *Daily Period of Illumination (illuminance* 240 *lm/sq. ft.)*.—The effect of daily period of illumination was less complex. When the illuminance was 240 lm/sq. ft. flies under a long daily period matured eggs more rapidly, fed more, and laid the mature eggs that were in their ovaries more readily than those under a shorter daily period of illumination.

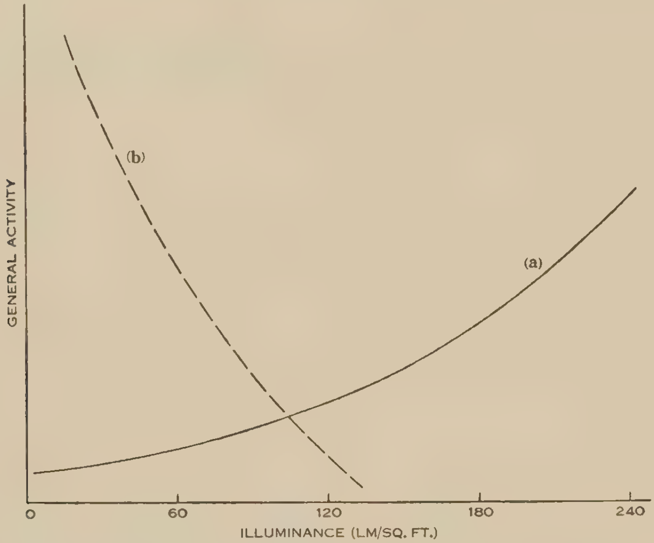

Fig. 8.—Hypothetical relationship between general activity and illuminance. (*a*) Line representing increasing general activity due to increasing illuminance; (*b*) represents increasing general activity as dusk illuminance is approached from a higher illuminance.

The number of hours of illumination each day determined the amount of feeding which in turn influenced the rate of maturation of eggs. Few eggs were laid by mature flies when they were kept in darkness. The period of illumination thus controlled the number of eggs the flies laid.

(*b*) *The Fecundities of Flies under Each Illuminance and Daily Period*

For the purposes of this discussion, the fecundity of flies under an illuminance of 240 lm/sq. ft. for 7½ hr/day is taken as a standard.

(i) 120 *Lm/Sq. Ft. for* 7½ *Hr/Day*.—To the end of the 7th week of adult life, the fecundity of flies under 120 lm/sq. ft. was about one-fifth that of flies under 240 lm/sq. ft. The major cause of this was the difference in the ages at which the flies mated. Flies under 120 lm/sq. ft.

mated, on the average, 23 days later in life than did those under 240 lm/sq. ft. and some were still unmated at the end of the 7 weeks. Since mated females developed and laid eggs more rapidly than virgins, this effect on mating meant that the flies produced many more eggs under 240 than under 120 lm/sq. ft. A less important factor was that virgin females under 240 lm/sq. ft. developed eggs 1½ times as rapidly as those under 120 lm/sq. ft. The effect of light on egg laying was unimportant.

(ii) 60 *Lm/Sq. Ft. for* 7½ *Hr/Day.*—The fecundity of flies under 60 lm/sq. ft. was not significantly different from that of flies under 240 lm/sq. ft. Flies under these two illuminances matured eggs at about the same rate, mated at about the same age, and laid their eggs equally as readily

(iii) *Constant Darkness.*—Flies kept in darkness laid no eggs during the first 7 weeks of adult life. Virgin females developed no eggs. Even when mature flies were exposed to dusk illumination after 24 hr of darkness they did not mate. Darkness greatly reduced the number of eggs laid by mature mated females.

(iv) 240 *Lm/Sq. Ft. for* 2 *Hr/Day.*—In 7 weeks flies kept under 240 lm/sq. ft. for 2 hr/day laid about 7 per cent. of the number of eggs laid by flies under the same illuminance for 7½ hr/day. Flies exposed for 2 hr/day developed eggs about one-quarter as rapidly as those exposed for 7½ hr/day and mated much later in life. Only a little more than half of the flies illuminated for 2 hr/day had mated by the end of the 7th week. The shorter daily period limited oviposition; flies illuminated for 2 hr/day retained more eggs in their ovaries than did those illuminated for 7½ hr/day. These three factors all contributed to the great difference between the fecundity of the flies in these groups.

(v) 240 *Lm/Sq. Ft. for* 4 *Hr/Day.*—Flies kept under 240 lm/sq. ft. for 4 hr/day laid about half as many eggs during the first 7 weeks of adult life as those exposed for 7½ hr/day. Those illuminated for 4 hr/day developed eggs about two-thirds as rapidly as those illuminated for 7½ hr/day. The age at which the flies mated was little affected. Egg laying may have been slightly inhibited in flies under illumination for 4 hr/day. Despite their slower rate of maturation of eggs, these flies were found to have retained a slightly greater number of eggs than those illuminated for 7½ hr/day.

The way in which light affects the fecundity of *S. tryoni* is very different from the way in which temperature affects the fecundity of insects. Temperature affects fecundity and other functions of insects by affecting the metabolic rate, whereas light affected fecundity of *S. tryoni* by influencing the behaviour of the flies. The different rates of egg maturation under different illuminances and daily periods were due to the effect that light had on the amount of food eaten. The rates of development and egg laying were affected by mating, and the age at which the flies mated was affected by light. The effect of light on the act of egg laying was important in limiting the numbers of eggs laid by flies kept under short daily periods of illumination.

These results indicate that, in any study of the effect of light on the ecology of an insect, it might be important to study the behaviour of the insect thoroughly so as to differentiate between a direct type of effect, such as temperature has on insects, and an indirect type of effect such as light was shown to have on the fecundity of *S. tryoni.*

It is not possible to discuss these results in relation to those obtained for other insects because few examples of light affecting the fecundity of insects have been reported, and I do not know of any in which the effect has been analysed sufficiently to indicate how light acts.

The following is a brief summary of these examples. *Bruchus obtectus* Say, the bean weevil, lays more eggs when kept in darkness than when kept in light. The higher the illuminance, the smaller is the number of eggs laid (Menusan 1935). Way, Smith, and Hopkins (1951) showed that the tomato moth *Diataraxia oleracea* (L.) has lower fecundity when kept either in constant darkness or in constant light than when illuminated for 8 or 16 hr/day. They also showed that *Pieris brassicae* (L.) required direct sunlight for mating and oviposition, and that oviposition in *Phaedon cochlaeriae* (Fabr.) was retarded by constant darkness.

V. ACKNOWLEDGMENTS

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I wish to thank Dr. L. C. Birch, Reader in Zoology, University of Sydney, for his guidance throughout the course of the work, and those at the University of Sydney and C.S.I.R.O., Canberra, who commented on the manuscript of this paper.

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THE PARASITIC LIFE-CYCLE OF *HAEMONCHUS PLACEI* (PLACE) RANSOM (NEMATODA: TRICHOSTRONGYLIDAE)

By K. C. Bremner*

(*Manuscript received June* 1, 1956)

Summary

The parasitic life-cycle of *Haemonchus placei* (Place 1893) Ransom 1911 is described and compared with that of *H. contortus* (Rudolphi 1803) Cobb 1898.

The third ecdysis of *H. placei* larvae occurred 36-76 hr after infestation, and the fourth and final moult occurred 11-14 days after infestation in the majority of larvae. Many third- and fourth-stage larvae penetrated deeply into the gastric glands of the mucosa. A small proportion of larvae did not develop beyond the early fourth stage, even after the majority had become adult.

The pre-patent period of *H. placei* was estimated to be about 11 days longer than that of *H. contortus.*

I. Introduction

Recent observations by Roberts, Turner, and McKevett (1954) and by Bremner (1955) have indicated that the so-called ovine and bovine "strains" of *Haemonchus contortus* are distinct species. The name *H. contortus* (Rudolphi 1803) Cobb 1898 was retained for the species commonly found in sheep and goats, and the name *H. placei* (Place 1893) Ransom 1911 was referred to the species commonly found in cattle.

In view of the recognition of *H. placei* as a distinct species and of its importance as a parasite of cattle, studies have been carried out to discover whether its parasitic life-cycle differs in any way from that of *H. contortus* as reported by Veglia (1915) and Stoll (1943).

II. Methods

Calves were reared worm-free in concrete pens, and when 2-3 months old were each given approximately 250,000 larvae of *H. placei* by mouth. At intervals after infestation one calf was slaughtered, the abomasum removed, the contents collected, and a portion of its wall was taken for histological examination. The gastric mucosa was thoroughly washed and kneaded under a stream of water to ensure removal of any immature forms. After these washings had been added to the abomasal contents, the pooled material was thoroughly mixed by means of a stream of compressed air, and a sample of approximately 100 ml of the suspension was removed. Small subsamples were then diluted in a Petri dish and examined systematically under a dissecting microscope. All larval or adult stages collected from the sample were transferred to hot 70 per cent. alcohol, which fixed the worms in an extended position. After fixation, the worms were cleared in the usual mixture of alcohol and glycerine and mounted in glycerine. Measurements of the larvae were made with the aid of a camera lucida.

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III. The Parasitic Life-cycle

No differences were found in the morphology of the various parasitic larval stages of *H. placei* compared with similar cycle stages of *H. contortus* as described by Veglia (1915) but the rate of development differed and this will be referred to again later.

(i) *Development at* 36 *Hr.*—The first calf was examined 36 hr after infestation. There were no detectable lesions in the wall of the abomasum at this time. Of 121 larvae recovered from the random sample of abomasal washings, more than 99 per cent. (120 larvae) were exsheathed third-stage larvae. One larva had already moulted to the fourth stage. Such fourth-stage larvae are readily recognized by their characteristic buccal capsules (Veglia 1915). Sections of the mucosa revealed that many exsheathed third-stage larvae had migrated into the pits of the gastric glands (Plate 1, Fig. 1), and that some had penetrated even deeper into the tubules of the glands, reaching almost to the muscularis mucosa. However, such larvae had caused no tissue damage, and no evidence could be seen of any reaction to their presence. The length of 100 of these larvae ranged from 620 to 760 μ (mean 704 μ, S.D. 31.2).

(ii) *Development at* 48 *Hr.*—On macroscopic examination, the surface of the gastric mucosa appeared normal. Examination under a dissecting microscope of an excised piece of mucosa revealed many larvae lying on the surface of the mucosa, and observations under higher magnifications showed that these were in the fourth stage of development. Of 255 larvae collected at random from the gut washings, 22.4 per cent. were found to be in the fourth larval stage. The remaining third-stage larvae were in the process of moulting, and in many of them the new fourth-stage cuticle had developed, while the old third-stage skin had become detached from the new cuticle and enveloped the larvae only loosely. Such larvae showed the details of the third ecdysis in all its phases. First the third-stage skin becomes progressively looser about the body of the worm. This process begins with equal frequency at the anterior or posterior end. The loose sheath of skin then swells out in a balloon-like manner in the region surrounding the oesophageal bulb until the third-stage skin ruptures either transversely or longitudinally in this region. The body of the young fourth-stage larva protrudes through the point of rupture and the head is drawn free from the anterior end.

Apparently some difficulty is experienced in freeing the newly developed buccal capsule, as the anterior portion of the old skin is often deeply invaginated by the withdrawal of the larvae.

The total length of 100 third-stage larvae collected at this time ranged from 610 to 770 μ (mean 702 μ, S.D. 31.2). Measurements of 100 infective larvae of *H. placei,* obtained by faecal culture and exsheathed in a 1: 20 dilution of Milton's solution, gave a range of length from 610 to 750 μ (mean 694 μ, S.D. 35.6). Comparison of these lengths with those obtained from parasitic third-stage larvae which were beginning to moult showed that no growth of the larvae took place during their first 2 days of parasitic existence.

The lengths of 50 fourth-stage larvae, collected 48 hr after infestation, ranged from 620 to 860 μ (mean 715 μ, S.D. 63.9), which indicates that growth of the fourth-stage larvae commenced shortly after the third ecdysis is completed.

(iii) *Development at* 76 *Hr.*—Seventy-six hr after infestation evidence of an inflammatory reaction to the larvae was observed, the gastric mucosa exhibiting slight hyperaemia and a catarrhal exudate. Sections of the mucosa showed that many larvae had embedded their heads deep within the gastric pits while the greater length of their bodies lay coiled within the exudate on the surface of the mucosa (Plate 1, Fig. 2). Little or no tissue damage had occurred.

Of the 208 larvae obtained at this time by random sampling of the gut washings all were in the fourth stage, and exhibited a detailed anatomy similar to that described by Veglia for larvae of *H. contortus* 3 days after infestation of sheep. Fifty-five of these larvae were measured, and their lengths fell within the range 720-1200 μ (mean 933 μ, S.D. 90.5).

(iv) *Development at* 10 *Days.*—Ten days after infestation, the wall of the abomasum showed numerous blood clots up to 4 mm in diameter, and when the catarrhal exudate and blood clots were removed, the mucosa displayed a generalized hyperaemia.

Histological examination revealed that many larvae still lay with the head inserted in a gastric pit while the main body of the worm lay coiled within a blood clot on the surface of the mucosa. Apart from the generalized hyperaemia which was more intense in the immediate vicinity of the larvae, little tissue reaction was detected. There was some infiltration of the mucosa by mononuclear cells and a few eosinophils were observed in its lower layers.

Examination of 141 worms obtained by random sampling revealed that all were still in the fourth stage of development, but there was great variation in the degree of their development. Seventy per cent. of them displayed a gross morphology similar to that described by Veglia for *H. contortus* larvae 7-10 days after infestation, whereas 25 per cent. appeared identical in this respect with *H. contortus* at 5-6 days. The remaining 5 per cent. had undergone little or no development past that seen in infestations 3-4 days old. It may be noted that the total infestation in this animal was estimated by counts on random samples to approximate 120,000 worms.

(v) *Development at* 13 *Days.*—At this time, the abomasum displayed a gross appearance similar to that seen 10 days after infestation. Sections of the abomasum showed that feeding by adult worms had resulted in erosion of circumscribed areas of the mucous epithelium. The heads of the worms were attached to the surface of the eroded mucosa and were surrounded by a thick coagulum of blood, mucus, and desquamated epithelial cells (Plate 1, Fig. 3). Although the nature of the tissue reaction at this time was similar to that found at 10 days, the inflammation at 13 days was much more intense and greater numbers of mononuclear and eosinophil cells had infiltrated the mucosa.

Of 114 worms examined at random from the gut washings, 66 per cent. had developed to the adult stage, 9 per cent. were in the process of moulting from the fourth stage, while 25 per cent. were still in the fourth stage. It is of interest that of these 28 fourth-stage larvae eight were still in the early phases of fourth-stage development. Male and female worms apparently grew at the same rate, since the sexes were represented in approximately the same proportions at any one stage of growth.

(vi) *Development at* 15 *Days.*—The pathology of the abomasum 15 days after infestation was essentially similar to that found at 13 days. A random sample of the infestation showed that of 108 worms present, 103 were adult *H. placei,* while five had not developed beyond the early fourth stage. No eggs were seen in the uteri of any of the young adult females, and no worms were found in copulation.

IV. Discussion

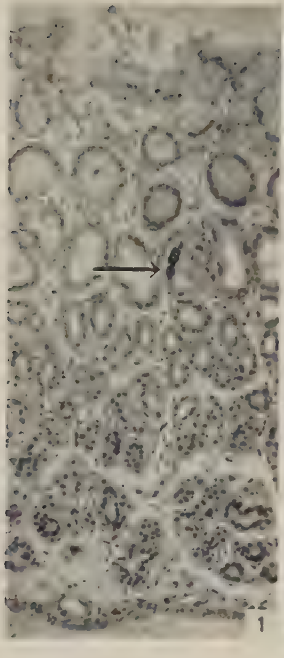
When the development of parasitic larvae of *H. placei* was compared with that described for *H. contortus* by Veglia (1915), no differences in organogenesis could be found. Whereas Veglia referred to the presence of cervical papillae in adult *H. contortus* but did not describe them in fourth-stage larvae, examination of *H. placei* larvae at various stages of development revealed that cervical papillae first appeared in larvae about 5 days after infestation. Also, while Veglia states that "larvae in the third ecdysis, or just after completion, were found to be from 750 to 850 μ in length", the present author found *H. placei* at this time to vary from 620 to 860 μ in length. It is difficult to reconcile Veglia's measurements with ours, particularly as Mönnig (1931) quotes a range of 694-772 μ for infective larvae of *H. contortus,* and Keith (1953) and Roberts, Turner, and McKevett (1954) have shown that the infective larvae of *H. placei* are longer than those of *H. contortus,* even when the difference in extension of the sheath beyond the tail of the larvae has been taken into consideration.

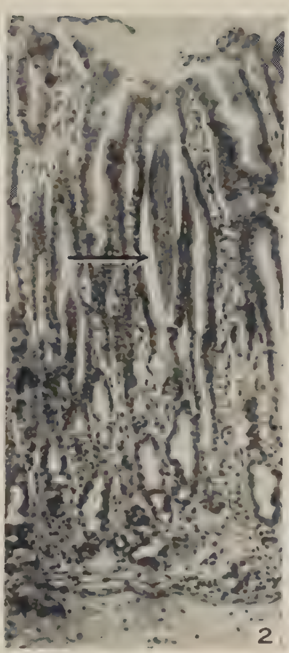
In these experiments, the third ecdysis of *H. placei* commenced approximately 36 hr after infestation and was complete by 76 hr. Veglia gave similar times for the third ecdysis of *H. contortus*. *H. placei* larvae exhibit a histotropic phase similar to that described for *H. contortus* by Stoll (1943). An unexpected feature of fourth-stage development was the depth to which many larvae penetrated within the gastric glands, one larvae being seen which had penetrated to the muscularis mucosa. In spite of this activity of fourth-stage larvae there was little tissue damage and it would seem that the feeding habits of this stage are concerned more with blood-sucking than with ingestion of host tissue; no erosion of the mucosa was seen that was in any way comparable to that caused by adult worms.

It was found that 10 days after infestation no larvae had moulted to the adult stage, but by 13 days 66 per cent. were adult, and 95 per cent. had become adult by 15 days. Therefore the majority of *H. placei* presumably undergo their final ecdysis 11-14 days after infestation. Veglia reported that this moult of *H. contortus* occurs between the ninth and eleventh day, and that by the twelfth day all larvae have reached the adult stage. Thus the duration of the fourth larval phase of *H. placei* is slightly longer than that of *H. contortus*.

Moreover, while Veglia stated that it "was not uncommon to find eggs (of *H. contortus*) in the faeces of the host even on the fifteenth day", Roberts (personal communication) found that eggs of *H. placei* usually do not appear in the faeces until 26-28 days after infestation. To ascertain whether a similar difference between pre-patent periods would be exhibited when both species were present in the same host, a worm-free lamb was dosed simultaneously with 7000 infective larvae of *H. contortus* and 7000 of *H. placei*. Whereas larvae of *H. contortus* were first obtained from faecal cultures prepared 19 days after infestation of this lamb, those of *H. placei* did not appear until faeces were cultured 30 days after infestation. It would appear, therefore, that the pre-patent period of *H. placei* is about 11 days longer than that of *H. contortus*.

The inhibition of development of a low percentage of fourth-stage larvae is of some interest. Roberts (unpublished data) found numerous fourth-stage larvae still present in calves 14-17 weeks after infestation with a single dose of 50,000 larvae of *H. placei*, and Taylor and Michel (1953) consider that the phenomenon of arrested development during parasitic life is probably a common occurrence among parasitic nematodes. These authors suggest that such inhibited larvae are unable to continue their development until there is "living room" for them in the lumen of the gut, this living room being obtained by the removal of adults. It would appear, however, that the inhibition could be the result of one of two factors: either those larvae which are most developed reach a stage at which they produce a substance which has a direct inhibitory effect on the growth of less developed larvae, or the inhibition may be the result





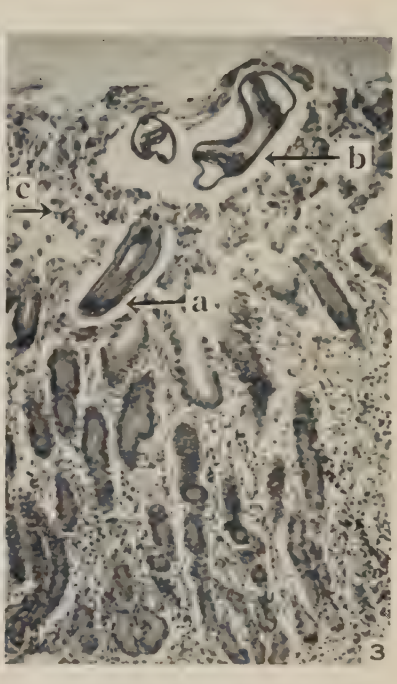


Fig. 1.—Third-stage larva of *H. placei* in the gastric mucosa of a calf 36 hr after infestation. × 105.

Fig. 2.—Section through the head of a fourth-stage *H. placei* larva in a gastric pit 76 hr after infestation. × 105.

Fig. 3.—Section through the head region of an adult *H. placei* attached to the gastric mucosa of a calf 13 days after infestation. *a*, Cephalic region of worm; *b*, coiled body of worm in section; *c*, desquamated epithelial cells. × 105.

of a host reaction to some activity or secretion of the more developed larvae.

However, it is not suggested that a similar mechanism is necessarily a major factor in animals which are constantly exposed to infective larvae on infested pastures. The answer to this problem must await further work on the biochemistry and immunology of host-parasite relationships.

V. ACKNOWLEDGMENTS

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THE PARAMPHISTOMES (TREMATODA) OF AUSTRALIAN RUMINANTS

III. THE LIFE-HISTORY OF CALICOPHORON CALICOPHORUM (FISCHOEDER) NASMARK

By P. H. DURIE*

(*Manuscript received March* 13, 1956)

Summary

A description of the life-history of *Calicophoron calicophorum* (Fischoeder 1901) Näsmark 1937 is given, and the larval stages of this parasite within the snail intermediate host *Pygmanisus pelorius* (Iredale 1943) are described.

The pre-patent period for this fluke in a lamb was found to be in the vicinity of 80-95 days.

I. INTRODUCTION

The species of paramphistomes recorded by Durie (1951) from Australian ruminants include *Ceylonocotyle streptocoelium* (Fischoeder 1901) Näsmark 1937, *Calicophoron calicophorum* (Fischoeder 1901) Näsmark 1937, and *Paramphistomum ichikawai* Fukui 1932. The life-histories of *C. streptocoelium* and *P. ichikawai* were subsequently determined by the same worker (Durie 1953) and involve the planorbid snails *Glyptanisus gilberti* (Dunker 1848) and *Segnitilia alphena* (Iredale 1943) respectively as intermediate hosts.

Although *C. calicophorum* is an extremely common and widespread species, its life-history has remained unknown until recently when its intermediate host was found to be a third species of planorbid snail, namely, *Pygmanisus pelorius* (Iredale 1943). This species of snail was also found to be acting as the intermediate host for an amphistome fluke of frogs, belonging to an unidentified species of *Diplodiscus*.

II. THE INTERMEDIATE HOST

The investigations reported in this paper were initiated at Amberley Field Station near Ipswich, which is attached to this Laboratory, where a calf was found to be carrying a pure infestation of *C. calicophorum*. The infestation comprised, in addition to mature adults in the rumen, a number of immature flukes in the small intestine indicating that metacercariae had been ingested shortly before the death of the host. A survey of the area over which the calf had grazed revealed numbers of a small planorbid snail, *P. pelorius* (Fig. 1), in semi-permanent water-holes. Although the snails were not particularly numerous in any one place they were widely scattered throughout the area.

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Two types of amphistome cercariae, a large white cercaria and a small black type were found in these snails. Eighty per cent. of the snail population was found to be infested with these larval amphistomes, and approximately half of the infestations comprised the small black type of cercaria. These readily encysted and when the cysts were fed *per os* to a lamb subsequent examination showed that they were metacercariae of *C. calicophorum*.

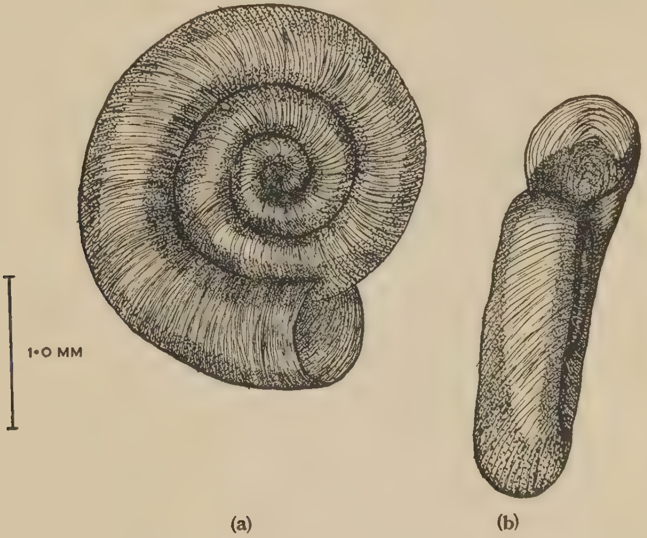

Fig. 1.—*Pygmanisus pelorius*: (*a*) view showing lower surface, (*b*) view showing mouth opening.

P. pelorius is similar in shape to the other members of the Planorbidae and is very similar in general appearance to *G. gilberti*, the intermediate host of *C. streptocoelium*. However, it may be distinguished from this species by the absence of a keel surrounding the periphery of the shell, and by the circular as opposed to the oval shape of the mouth of the shell. The shape of *P. pelorius* is distinctly different from that of *S. alphena*, the intermediate host of *P. ichikawai*, which is convex above and flat to concave below. *P. pelorius* occurs chiefly in small, semi-permanent waterholes, such as "melon holes", and does not appear to inhabit large bodies of water, such as swamps and dams, which are the typical habitats of the intermediate hosts of *C. streptocoelium* and *P. ichikawai*. It is evidently adapted to survive long periods of dry conditions, for, in one instance, 24 hr after heavy rain snails were found to be numerous in melon holes which had been completely dry for 3 months. This ability to withstand dry conditions makes this species a particularly efficient intermediate host. Infested snails appear to survive prolonged dry periods as readily as uninfested ones, and will secrete cercariae 24 hr after rain has fallen.

III. THE LARVAL STAGES OF C. CALICOPHORUM

Generally, the larval stages of *C. calicophorum* are similar to the corresponding stages described by Durie (1953) for the two other species of amphistomes found in Australian ruminants. Although sporocysts were not seen in infested snails, this is considered due to the fact that this stage was not present in the snails examined, rather than to its absence in the life-cycle of the parasite.

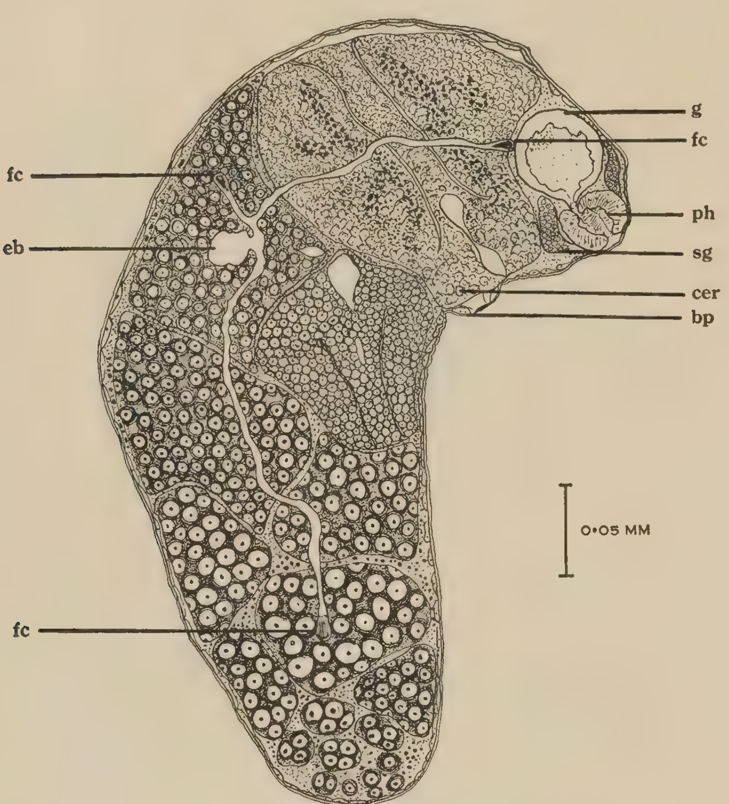

Fig. 2.—*Calicophoron calicophorum*: mature redia (lateral view); *bp*, birth pore; *cer*, cercaria; *eb*, excretory bladder; *fc*, flame cell; *g*, gut; *ph*, pharynx; *sg*, salivary gland.

The Redia (*Fig.* 2).—A fully mature redia measured 408 μ in length and 112 μ in width and contained 13 embryos in addition to germ balls at the posterior end of the body. The excretory system consists of three pairs of flame cells connected by ducts on each side and opening from a small vesicle or bladder situated slightly posterior to the middle of the body in the vicinity of the middle pair. The structure and position of the excretory system is similar to that described for other paramphistome rediae in Australian ruminants (Durie 1953). The redia of *C. ijimai* in New Zealand was reported to have five pairs of flame cells arranged symmetrically (Jonathan 1952) and so differs from the present species in this character.

The Cercaria (*Fig.* 3).—The cercaria is released from the redia while still immature and subsequent development takes place in the host tissues. The development of the pigmentation and internal systems appears similar to that of other paramphistome cercariae.

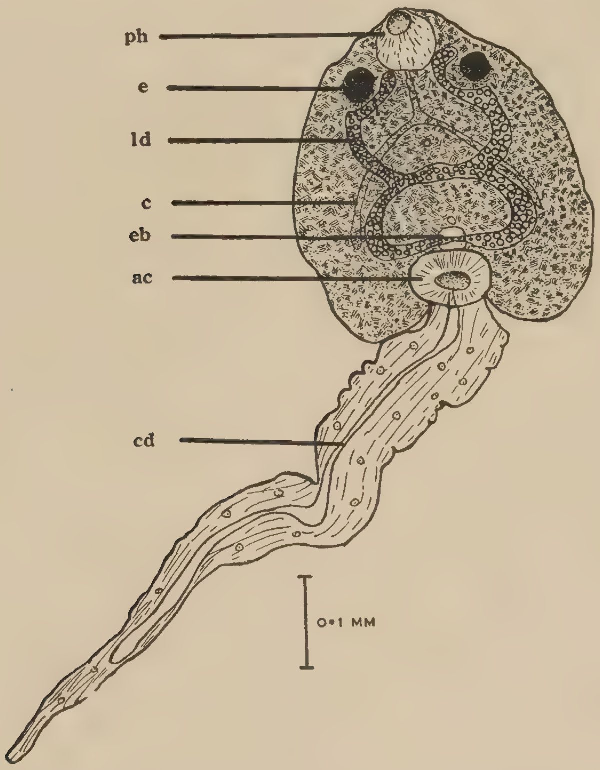

Fig. 3.—*Calicophoron calicophorum*: mature cercaria showing internal structure (ventral view); *ac*, acetabulum; *c*, caecum; *cd*, caudal excretory duct; *e*, eyespot; *eb*, excretory bladder; *ld*, main lateral excretory duct; *ph*, pharynx.

The mature cercaria is released from the snail through the pulmonary aperture and swims actively on release into the water. It is attracted to yellow light and encysts readily on a yellow illuminated surface in the same manner as described by Durie (1955) for other paramphistome cercariae. The cercaria is dark brown to black in colour and possesses two conspicuous eyespots. When fixed in chloral hydrate in the manner previously described (Durie 1953), it measures 277 μ in length and 164 μ in width (262-294 $\mu \times$ 152-184 μ). The tail measures 494 μ in length when fully extended. The acetabulum is 77 μ in diameter.

The internal structures are difficult to observe because of the opacity of the pigmentation and cystogenous cells, but the major portions of the excretory system may be seen in specimens flattened under a cover slip. The excretory system possesses a cross anastomosis between the large lateral excretory ducts in a manner typical of the other paramphistome cercariae. The course and structure of the large lateral ducts are similar to those described previously (Durie 1953), and there is a small projection on the cross anastomosis which probably represents a poorly-developed median evagination. No lateral evaginations are present surrounding the eyespots, but in some specimens a slight outward projection, probably representing a greatly-reduced lateral evagination, may be seen.

The lateral excretory ducts open into a well-defined excretory bladder situated near the anterior margin of the acetabulum which opens on the dorsal surface of the body through the excretory pore. The caudal excretory duct runs through the tail to open at the posterior end in the usual manner. The large lateral ducts of the excretory system contain numerous excretory granules.

The digestive system is inconspicuous due to its very delicate structure and to the opacity of the body, and may be seen only in grossly flattened specimens. The pharynx leads into a fine oesophagus which bifurcates at the level of the cross anastomosis, and the thin caeca extend backwards to a point level with the anterior margin of the acetabulum.

The cercaria of *C. calicophorum* may be distinguished from that of *P. ichikawai,* which it resembles in shape when flattened under a coverslip, by the absence of lateral evaginations around the eyespots. It may be readily distinguished from that of *C. streptocoelium* by the shape assumed under a coverslip and also by the difference in size (Durie 1953).

The Metacercaria.—The metacercaria resembles that of the other species described previously (Durie 1953). It is dark brown to black in colour and measures 179.4 μ (125-202 μ) in diameter. The average diameter of the embryo is 133 μ (124-147 μ). The cyst measures approximately 120 μ in height.

IV. THE PRE-PATENT PERIOD

Cysts collected from infested snails from the field were fed to a lamb *per os* for the identification of the adult stage. The initial dose of cysts was administered on July 12, 1955, and subsequent doses were given on July 27, 1955 and August 22, 1955. Paramphistome eggs were first detected in the faeces of this lamb on October 17, 1955. At slaughter, the lamb was found to be harbouring 12 specimens of *C. calicophorum* in the rumen. These specimens were of two sizes, 10 being large mature flukes averaging 5.8 mm in length and two being small and immature with a mean measurement of 3.1 mm in length when fixed in Carnoy's fluid. The large specimens were evidently derived from the first or second feeding, so that it seems that the pre-patent period for this fluke is in the vicinity of 80-95 days. Ova recovered from the 10 mature specimens averaged 115 × 69 μ. The size of these eggs is smaller than that reported for this species previously (Durie 1951), but, as the eggs were from recently-matured specimens, smaller eggs might be expected, as reported by Bennett (1936).

V. ACKNOWLEDGMENTS

The author wishes to thank Dr. F. H. S. Roberts, Officer-in-Charge of this Laboratory, for helpful advice and criticism so freely given during the course of these investigations. Thanks are also given to Mr. B. C. Cotton, Conchologist, South Australian Museum, for identification of snail specimens.

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TAXONOMY AND BIOLOGY OF THE GENUS *ISOMETROIDES* KEYSERLING (SCORPIONIDA)

By Barbara Y. Main*

(*Manuscript received March* 21, 1956)

Summary

From an examination of specimens of the scorpion *Isometroides* Keyserling collected in Western Australia, South Australia, and New South Wales and a study of the literature, it is concluded that two described species must be regarded as one. *I. angusticaudus* Keyserling is considered a synonym of *I. vescus* (Karsch).

The genus represents a unique adaptive level, especially in its specialized feeding behaviour. It is distributed throughout the semi-arid inland. These facts make it difficult to find a geographically imposed isolation whereby the genus, once established, could have speciated.

Field observations on this rare scorpion are presented. It is widespread, occurring in woodland and semi-arid country. In habit it is terrestrial, vagrant, and is specialized for feeding on burrowing spiders.

I. Introduction

The endemic Australian genus of scorpions, *Isometroides,* is close to the genus *Lychas,* and contains two described species. *I. vescus* (Karsch) 1880, is restricted in the south-west of Western Australia within the area north of a line drawn from Serpentine to Dudinin and south of a line from Geraldton to Kalgoorlie, and *I. angusticaudus* Keyserling, 1885, is found north of this line and over the rest of Australia (Glauert 1925). Both species appear to be rare, a total of only 16 specimens is reported in the literature, these having reached museums over the course of some 40 years. There are no records subsequent to Glauert (1925).

During the past 4 years while engaged in field collecting of mygalomorph spiders in Western and South Australia the author obtained 21 specimens of *Isometroides* and two additional specimens were received from Mr. W. B. Malcolm to whom grateful thanks are offered. Difficulty in naming these specimens led the author to a critical review of the genus with a view to clarifying the status of the species. The results of this study, together with observations on the biology of the scorpion, are reported below.

II. Systematics

Isometroides and *Lychas* are the only Australian representatives of the subfamily Buthinae. These two genera are readily distinguished as follows:

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Lychas: aculeus of sting with a tooth below, 5th caudal segment with keels (except *L.*(*Hemilychas*) which has the same form as *Isometroides*).

Isometroides: aculeus without tooth, 5th caudal segment smooth, shining, and unkeeled.

Lychas is a large and widely-distributed genus. It is possible that *Isometroides,* as a genus, has been derived from *Lychas* by biological specialization and morphological accentuation of the characters present in the subgenus *L.* (*Hemilychas*). The above characters can be construed as indicating the intermediate nature of the monotypic subgenus *L.* (*Hemilychas*). In addition, the vesicle-aculeus junction of some specimens of *Isometroides* is marked by a slight irregularity. This is quite pronounced in some of the author's specimens (Fig. 1), and might be interpreted as representing a vestigial tooth. However, speculation on the relationships of these scorpions is premature until more specimens of *L.* (*Hemilychas*) *alexandrinus* have been collected and more is known of the biology of this and other *Lychas* species.

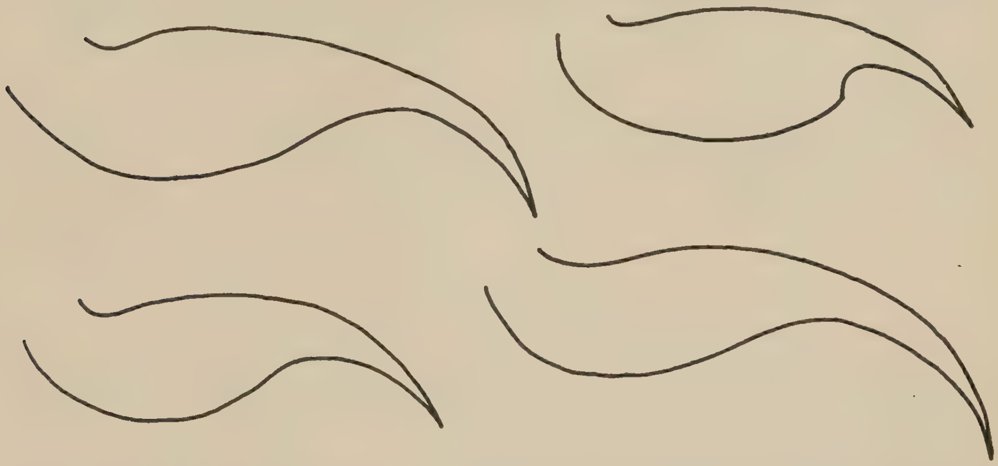

Fig. 1.—Outline of 6th caudal segment of selected specimens of *Isometroides* to illustrate the variation and difficulty of determining the end of vesicle and beginning of aculeus.

Genus ISOMETROIDES Keyserling

Glauert (1925) reviews the genus *Isometroides,* gives descriptions of the genus and both species, and lists all the references. Repetition of the above information is therefore unnecessary. The few diagnostic features of the two species *I. vescus* (Karsch) and *I. angusticaudus* Keyserling indicated by Karsch (1880), Keyserling (1885), Kraepelin (1899, 1916), and Hirst (1907) have been summarized by Glauert (1925, p. 113) and are presented here in Table 1. The foregoing six references include all the literature on the two species.

The 23 specimens in the author's collection were examined, noting each of the characters listed in Table 1, i.e. texture of surface and presence or absence of keels on 4th caudal segment, nature of surface of 5th caudal segment, aculeus-vesicle ratio of sting, and number of teeth on pectines, and, in addition, the dimensions and sex of the animals. The data were analysed in tabular form and the relevant results are summarized below.

TABLE 1

DIAGNOSTIC CHARACTERS OF I. VESCUS (KARSCH) AND I. ANGUSTICAUDUS KEYSERLING, SUMMARIZED FROM GLAUERT (1925)

I. vescus	*I. angusticaudus*
Fourth caudal segment keelless or very feebly keeled, intercarinal surfaces smooth	Fourth caudal segment with 8 well-developed keels and short accessory keels, intercarinal surfaces granular
Surface of 5th segment punctured, smooth, and shining	Surface of 5th segment punctured and with rugosities
Aculeus as long as the vesicle (authors usually state aculeus and vesicle to be about equal in length)	Aculeus shorter than vesicle (authors usually state aculeus to be half length of vesicle)
Pectines with 23-26 teeth	Pectines with 21-23 teeth (Keyserling stated the type to have 20 teeth on each pectine)

(*a*) *Nature of 4th Caudal Segment*

There is no correlation between the presence or absence of keels and the smooth or granular condition of the intercarinal surfaces, therefore these are invalid diagnostic features.

(*b*) *Texture of Surface of 5th Caudal Segment*

Punctured and smooth in all specimens examined, irrespective of whether the other three diagnostic features were attributable to *I. vescus* or *I. angusticaudus.*

(*c*) *Aculeus-Vesicle Ratio*

The ratio varied considerably and many specimens were intermediate between the two species. In only three specimens did the aculeus and vesicle approach equality and in these the other characters were not all those of *I. vescus.* It appeared also that larger animals had a relatively shorter aculeus (i.e. in relation to vesicle). From an examination of Figure 1 it will be seen that it is difficult to determine where vesicle ends and aculeus begins. Some specimens show a marked junction between aculeus and vesicle, whereas others blend smoothly with no appreciable junction, and there are intermediates between the two extremes. Because this is a difficult character to measure accurately it is not a good diagnostic feature. Finally, it was obvious that the specimens with the proportions more or less definitive for one or the other species did not always show the obligatory correlation with the other diagnostic features.

(*d*) *Number of Pectine Teeth*

Many of the specimens had a different number of teeth on the two pectines. The number of teeth per pectine varied from 21 to 27. The results are summarized in Table 2 and show that on this character only two specimens could unequivocally be designated *I. angusticaudus.* But not all the other features of these specimens were those of *angusticaudus,* in particular the 5th caudal segment showed no rugosities.

TABLE 2

NUMBER OF TEETH ON EACH PECTINE OF 23 SPECIMENS OF ISOMETROIDES

No. of Teeth on Each Pectine		Frequency of Occurrence
21	22	1
22	23	1
23	23	3
23	24	2
23	25	1
24	24	2
24	25	2
25	25	5
25	26	2
26	26	1
26	27	1
27	27	1
26	Damaged	1

It is clear from this morphological analysis that the characters given for differentiating the two species *I. vescus* and *I. angusticaudus* occur together in some individuals and show a great deal of variation between individuals. It must be concluded that there is only one species. *I. vescus* (Karsch) has priority and *I. angusticaudus* Keyserling is to be regarded as a synonym of *I. vescus.* The only other synonym is *Isometrus vescus* Karsch, under which name the species was originally described (Karsch 1880). This name was emended to *Isometroides vescus* when Keyserling (1885) erected the genus *Isometroides.*

Sufficient specimens have not been collected to demonstrate localized geographic, clinal, or other variation.

III. BIOLOGY

There is no data on the biology of *Isometroides* in the literature. The author's field observations are summarized in Table 3. Of the 21 specimens observed by the author and the two collected by Mr. W. B. Malcolm, 18 were collected during daylight from spiders' burrows and, of these, 13 from burrows with trapdoor entrances. In four of the burrows the scorpions were actually still eating the spiders at the time of collection. In all except the two *Gaius* burrows it appeared that the

TABLE 3

SUMMARY OF FIELD OBSERVATIONS ON 23 SPECIMENS OF ISOMETROIDES

Locality and Date	Situation in which Specimen Collected	Notes
Perth, 35 miles east of, Toodyay Rd., 12.x.52	In unidentified spider's burrow, silk-lined, no trapdoor at entrance	No sign of spider in burrow
Mt. Dick, 17.vi.52	In trapdoor spider's burrow, undescribed *Aganippe* sp.	Spider destroyed
Bolgart, 18.vi.52	In unidentified trapdoor spider's burrow	No sign of spider in burrow
Bungulla, 9 miles north of, 12.vii.52	In trapdoor spider's burrow, undescribed *Aganippe* sp.	Scorpion freshly moulted, cast at bottom of burrow with specimen and spider remains
Minnivale, 20.vii.54	In burrow of *Gaius villosus* Rainbow	Scorpion above "sock",* spider intact below sock
Merredin, 5.xii.53 (collected by W. B. Malcolm)	Specimen on ground beneath a piece of tin	Specimen inactive, collected during daylight
Mullewa, 12 miles west of, 6.ix.54	In burrow of *Aganippe* (?) sp.	Abdomen of scorpion greatly distended
Morowa, 1.x.52	In trapdoor spider's burrow, *Arbanitis hoggi* (Simon)	Scorpion with greatly distended abdomen
Merkanooka, 11.v.53	In trapdoor spider's burrow, *Aganippe occidentalis* Hogg	Scorpion feeding on spider
Merkanooka, 11.v.53 (near above specimen)	In trapdoor spider's burrow, *A. occidentalis*	Scorpion feeding on spider
Newdegate, 26 miles east of, 23.v.55	In trapdoor spider's burrow, probably *A. latior* Cambridge	Spider destroyed, scorpion with distended abdomen
Newdegate, 26 miles east of, 23.v.55 (near above specimen)	In burrow of undescribed *Aganippe* sp.	Spider destroyed
Peak Charles, 25.v.55	In trapdoor spider's burrow, *A. occidentalis*	Spider destroyed
Bulong, 5 miles south-east of, 29.i.56	In burrow of *A. raphiduca* Rainbow & Pulleine	Cast skin only of scorpion, no trace of spider
Fraser Range, 73 mile peg, Eyre Highway, 9.xii.53	In burrow of diplurid spider, probably *Dekana* sp.	Scorpion feeding on spider
Randells, 15 miles east of, 25.i.56	In burrow of diplurid spider, probably *Dekana* sp.	No sign of spider apart from recently cast skin

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* Spiders of the genus *Gaius* have a special defence apparatus consisting of a loose lining in the lower part of the burrow. This is pulled down onto the spider, protecting it from disturbance from above. Details of this "sock" are given in a paper (B. Y. Main, in preparation) on the aganippinid trapdoor spiders (family Ctenizidae).

TABLE 3 (*Continued*)

Locality and Date	Situation in which Specimen Collected	Notes
Randells, 15 miles east of, 25.i.56	In the same burrow as above	No sign of spider apart from recently cast skin
Magooinya Rock (Balladonia Stn.), 10.xii.53	Scorpion running on bare ground	Collected at night (many spider burrows nearby)
Magooinya, 10.xii.53 (near above specimen)	In burrow of *Gaius hirsutus* Rainbow & Pulleine	Scorpion above sock, spider below sock
Mt. Ragged, at base, 14.xii.53	Running on bare ground	Collected at night (trapdoor spiders also collected from area)
Madura, 31 miles east of, on coastal plain, 28.viii.55	Running on ground	Collected at night (9.15 p.m.)
Ivy Tanks, 4 miles west of (Eyre Highway, S.A.), 23.xii.52	In burrow of *Lycosa* sp., burrow with trapdoor	Scorpion feeding on freshly-killed *Lycosa* specimen
Wilcannia, N.S.W., 5 miles east of, 20.xi.52 (collected by W. B. Malcolm)	On ground, under a stone	Inactive, collected during daylight

spiders had been eaten by the scorpions, since the burrows were in good condition and obviously not in disuse.

When kept in captivity in a glass jar an *Isometroides* specimen was fed on theridiid spiders which were dropped into the jar. The prey was stung and devoured while held in the pedipalps. Nevertheless, it seems from field observations that *Isometroides* is a terrestrial scorpion which has a specialized feeding behaviour in that it is a predator on burrowing spiders. This conclusion is not based on biased collecting (i.e. solely for Mygalomorphae) since during field work various terrestrial habitats such as under stones and logs were examined. Such situations frequently yielded *Lychas* specimens, but no *Isometroides* except the two specimens collected by Mr. W. B. Malcolm.

As already noted these scorpions rarely reach museum collections, presumably because they are not ordinarily seen by collectors. This is understandable because the species is active only at night, it is cryptozoic during the day, or remains in the burrow of the last prey. However, the rareness of *Isometroides* can be gauged from the fact that the author's collection of about 3000 burrowing mygalomorphs and more than 200 burrowing lycosids has yielded only 18 scorpions in their feeding situation. On only three occasions has more than one specimen been collected from any one locality, though in most situations not every observed spider burrow was excavated.

(*a*) *Distribution*

None of the localities listed in Table 3 extend the range of the genus as given in the literature (Glauert 1925). Further, no specimens have been found in the wetter forested south-western corner of Western Australia, although many mygalomorphs and other scorpions have been collected in this region. This scorpion appears to belong to the woodland, semi-desert, and possibly true desert regions of Australia, wherever burrowing spiders occur in sufficient numbers to support it.

IV. ACKNOWLEDGMENT

The above observations were made and the specimens collected while the author was in receipt of a University of Western Australia Research Grant.

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PALAEOZOIC AND MESOZOIC HEMIPTERA (INSECTA)

By J. W. Evans*

(*Manuscript received May* 21, 1956)

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* The Australian Museum, Sydney.

Summary

New species of Triassic Homoptera and Heteroptera from the Brookvale series of New South Wales and Mt. Crosby, Queensland, are described, one homopteron from the Upper Permian of Warner's Bay, N.S.W., and Homoptera previously recorded from Palaeozoic and Mesozoic strata in Australia and elsewhere are reviewed. New illustrations, made from type specimens, are given for some Australian species.

Representatives of the family Scytinopteridae, previously known only from Permian strata, are recorded from the Triassic.

Two forewings of uncertain affinities, but having venational features similar to hylicids, are ascribed to species in genera placed in a new family, the Hylicellidae.

For leaf-hoppers which are regarded as transitional between the Palaeozoic and Mesozoic faunas, a new family, the Stenoviciidae, is proposed, and another new family, the Chiliocyclidae, is proposed for a group of Mesozoic leaf-hoppers of wide distribution.

A forewing from the Triassic of Queensland is identified as that of a eurymelid and another as a cicadellid.

The earliest undoubted cercopid, so far recorded, is described from the Triassic; a new family, the Eoscarterellidae, is defined to comprise insects of probable cercopoid affinities, and the family Dysmorphoptilidae is transferred to the Cercopoidea.

As the genus *Palaeontina* Butler is considered not to be a homopteron, a new family name, the Cicadomorphidae, is proposed for large Homoptera with cicada-like wings, previously recorded only from the Jurassic of Europe and which formerly have been included in the family Palaeontinidae. A new genus and species belonging to the Cicadomorphidae is described from the Triassic of New South Wales.

The relationships of a new family, the Cicadoprosbolidae, and of the Mesogereonidae are discussed and both are considered to be allied to the Cicadidae.

Two new psylloids are described and also an aphid, the latter being the first representative of the Aphidoidea to be recorded from Triassic strata.

No new fulgoroids are described but problems associated with the determination of fulgoroid venation are discussed.

The genus *Actinoscytina* Tillyard is transferred from the Homoptera to the Heteroptera and together with three new genera ascribed to a new family, the Actinoscytinidae. The family Ipsviciidae, formerly regarded as belonging to the Homoptera is also removed to the Heteroptera. The family Dunstaniidae is reviewed in the light of a re-examination of type specimens. Fossil fragments, poorly-preserved specimens, and wings of uncertain position which have at some time been referred to the Homoptera, are listed, and some are discussed. Possible derivations and interrelationships of the various major groups of Homoptera are indicated by means of a chart.

INTRODUCTION

Through the courtesy of Professor W. H. Bryan, Department of Geology, University of Queensland, and at the suggestion of Mr. E. Riek, Division of Entomology, C.S.I.R.O., I have been privileged to study a large collection of fossil Hemiptera from Mt. Crosby, Queensland. The beds containing these fossils are Upper Triassic (Tindale 1945).

The Australian Museum has a magnificent collection of fossil insects from the Upper Permian (Belmont beds) and Middle Triassic (Brookvale beds) and a search of the Collection made on my behalf by Mr. H. O. Fletcher, Palaeontologist at the Museum, has yielded some interesting undescribed Hemiptera from both series.

The new material from Queensland and New South Wales is described in this paper. At the same time, the opportunity has been taken to review the previously-described Palaeozoic and Mesozoic Homoptera of the world and, where possible, to relate extinct forms to recent groups.*

In the past, most fossil insects have been described by palaeo-entomologists who, however wide their knowledge of extinct groups may have been, perforce lacked specialist knowledge of more than one or two recent orders of insects. Only in a few instances have fossil insects been studied by a worker with a comprehensive knowledge of recent representatives. For this reason, there is often but little correlation between knowledge of extinct and recent forms.

While the present author has a general interest in the order Hemiptera as a whole, he can claim specialist knowledge only of the superfamily Cicadelloidea. Hence, part of this contribution, especially those sections that relate to the Heteroptera, is presented with some diffidence.

As an aid to facilitate comparisons, all illustrations of wings have been shown facing the same way, irrespective of whether left or right wings have been actually preserved.

Suborder HOMOPTERA

Family ARCHESCYTINIDAE Tillyard

This family was created by Tillyard (1926*a*) for the wings of three species of auchenorrhynchous Homoptera from Lower Permian beds in Kansas. The three species were placed in two genera, *Archescytina* Tillyard and *Permoscytina* Tillyard. In the same paper, another family, the Permopsyllidae, was proposed for the wing of an insect, *Permopsylla americana,* which the author regarded as belonging to the Sternorrhyncha.

In 1931, Carpenter described a new genus of Archescytinidae, *Paleoscytina* (type species *P. brevistigma*), transferred *Permopsylla* Tillyard to this family, and described two new species which he ascribed to this genus. At the same time, he suggested that the Archescytinidae can have been comprised in neither the Auchenorrhyncha nor the Sternorrhyncha and proposed a new division of the Homoptera, the

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* After this paper had gone to press, reprints of several works on fossil Homoptera by H. E. Bekker-Migdisova, which had not previously been seen, were received from Moscow. As soon as these have been translated, a supplementary paper will be prepared for publication giving particulars of the new Russian material and recording any consequential nomenclatorial changes that may be necessary.

Paleorrhyncha to contain them. He suggested this division could be regarded as ancestral to insects in the two others. In arriving at this opinion, he was influenced by evidence supplied by parts of the body of a specimen of *Archescytina permiana,* in particular by the large antennae which had at least 25 segments.

In a later paper (Carpenter 1939), the same author discussed the affinities of the Archescytinidae. He supposed that, because one specimen of *Permoscytina kansasensis* had a long terminal abdominal process, which might represent a respiratory tube, insects in this family were aquatic. Accordingly, he endorsed his former opinion that the Archescytinidae can have belonged to neither of the divisions of the Homoptera still in existence and suggested further that neither could they have been ancestral to either.

Previously (Evans 1946*b,* 1948) I have suggested that the abdominal process of the Archescytinidae may be homologous with the long apical abdominal extension which occurs in both sexes of the aetalionid *Darthula hardwickii* Gray. The function of this extension, which is a prolongation of the 9th abdominal tergite, is unknown, but it is not respiratory. As it is evident from the structure of the head, the venation of the tegmen, and the well-developed tymbals that *D. hardwickii* is the most ancient surviving cicadelloid, it may be supposed that its apical abdominal extension is an archaic structure which has been retained and not a recent development. The presence of this process is not, however, the sole reason for considering a separate division of the Homoptera as unnecessary for the reception of the Archescytinidae and further ones will be discussed later.

Fossil insects which have formerly been ascribed to the following families are all regarded here as belonging to the Archescytinidae: Lithoscytinidae Carpenter; Permoscytinopsidae Zalessky; Uraloscytinidae Zalessky; Maueridae Zalessky; Maripsocidae Zalessky; Permopsyllidae Tillyard.

The family Archescytinidae as here recognized comprises 15 genera as follows: *Archescytina* Tillyard, *Permopsylla* Tillyard, *Permoscytina* Tillyard, *Paleoscytina* Carpenter, *Sojanoscytina* Martynov, *Ivascytina* Martynov, *Austroscytina* Evans, *Permoscytinopsis* Zalessky, *Uraloscytina* Zalessky, *Lithoscytina* Carpenter, *Maueria* Zalessky, *Maripsocus* Zalessky, *Permopsyllopsis* Zalessky, *Archeglyphis* Martynov, *Scytoneurella* Zalessky. In Figures 1*A-H,* the range of venational types occurring within the family are illustrated and these are discussed below.

The fore- and the hindwings resemble each other in venation and in most, but not in all known forms, in shape. While most described wings have a venational pattern similar to that of *Permopsylla permiana* (Fig. 1*B*), it is suggested that, except in one particular, the venation of *Ivascytina difficilis* (Fig. 1*A*) represents a more generalized development. In the latter wing, *Sc* lies alongside *R* and the 2 veins are approximately parallel with the costal margin from which they are not widely separated. R_1a extends approximately to the centre of the costal margin and R_1b and Rs to the apex of the wing. There is a crossvein between Rs and M; M has 4 branches and a crossvein joins M_{3+4} to Cu_1a. In the wing figured, Cu_1 has 3 branches and this is regarded as a minor anomaly without significance. It is found also in the wing of *P. anomala* (Fig. 1*C*) but the usual condition of Cu_1 is shown in the other illustrations in Figure 1. The clavus of the figured specimen of *I. difficilis* is incomplete but the normal development of 2 anal veins is shown in Figures 1*B* and 1*C*.

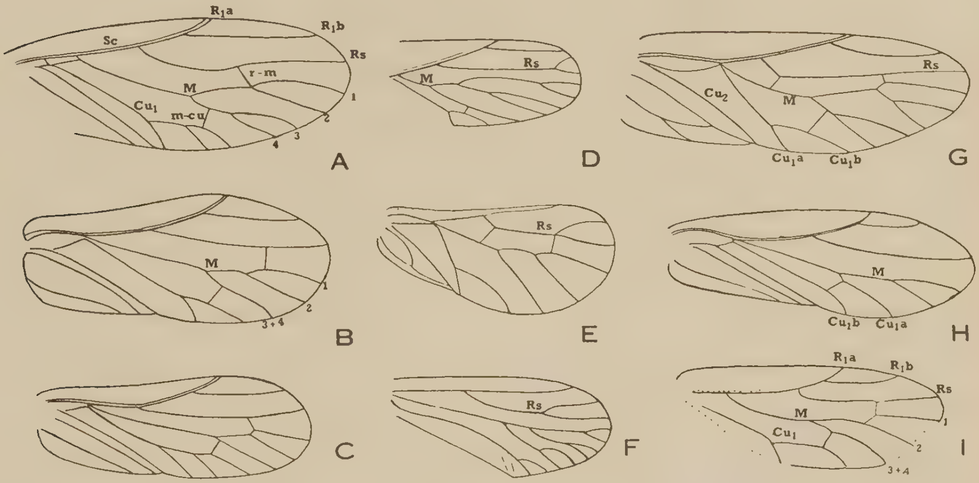

Fig. 1.—*A, Ivascytina difficilis; B, Permopsylla permiana; C, P. anomala; D, Uraloscytina prosboloides; E, Sojanoscytina latipennis; F, Archeglyphis crassinervis; G, Sojanoscytina grandis; H, Paleoscytina brevistigma; I, Austroscytina imperfecta.*

It will happen, in seeking to relate described wings to the various types of venation illustrated in Figure 1 and in subsequent figures, that forms will come together in series which differ from generic groupings. Furthermore, forms with the same generic designation will sometimes be placed in different families. As names for fossils based on wing impressions, in many instances, represent only venational types it would not at present prove helpful to change generic names nor to establish new synonymy.

IVASCYTINA DIFFICILIS Martynov

Fig. 1*A*

Ivascytina difficilis Martynov, 1933, Bull. Acad. Sci. U.R.S.S., Class. Sci. Math. et Nat., p. 889 (Permian, Russia).

The special features of this wing have been discussed above.

PERMOPSYLLA ANOMALA Carpenter

Fig. 1*C*

Permopsylla anomala Carpenter, 1933, Proc. Amer. Acad. Arts Sci. **68**: 438 (Lower Permian, Kansas).

The forking of Cu_1a is anomalous. The sharp proximal bend of Cu_1 in the direction of Cu_2 is a characteristic common to most Palaeozoic Homoptera. The 3-branched condition of M is typical of many of the representatives of the family.

PERMOSCYTINA TETRACLADA (Martynov)

Archescytina tetraclada Martynov, 1933, Bull. Acad. Sci. U.R.S.S., Class. Sci. Math. et Nat., p. 885 (Permian, Russia).

Permoscytina tetraclada (Martynov), Carpenter, 1939, Proc. Amer. Acad. Arts Sci. **73**: 53.

This wing has venation similar to that of *P. anomala*. Martynov regarded M as being 4-branched.

PERMOPSYLLA PERMIANA Carpenter

Fig. 1*B*

Permopsylla permiana Carpenter, 1931, Amer. J. Sci. **22**: 120 (Lower Permian, Kansas).

This wing represents the type of venation found in most of the recorded wings of archescytinids. M is reduced to M_1, M_2, and M_{3+4}.

The 8 wings recorded below resemble that of *P. permiana* in essential venational features, but some differ in shape and proportions.

ARCHESCYTINA PERMIANA Tillyard

Archescytina permiana Tillyard, 1926, Amer. J. Sci. **11**: 386 (Lower Permian, Kansas).

Archescytina permiana Tillyard, Carpenter, 1939, Proc. Amer. Acad. Arts Sci. **73**: 49.

ARCHESCYTINA MUIRI (Tillyard)

Permoscytina muiri Tillyard, 1926, Amer. J. Sci. **11**: 389 (Lower Permian, Kansas).

Archescytina muiri (Tillyard) Carpenter, 1939, Proc. Amer. Acad. Arts Sci. **73**: 49.

PERMOPSYLLA AMERICANA Tillyard

Permopsylla americana Tillyard, 1926, Amer. J. Sci. **11**: 391 (Lower Permian, Kansas).

Permopsylla americana Tillyard, Carpenter, 1931, Amer. J. Sci. **22**: 119.

PERMOPSYLLA GRANDIS Carpenter

Permopsylla grandis Carpenter, 1933, Proc. Amer. Acad. Arts Sci. **68**: 437 (Lower Permian, Kansas).

PERMOPSYLLA MINUTA Carpenter

Permopsylla minuta Carpenter, 1931, Amer. J. Sci. 22: 121 (Lower Permian, Kansas).

PERMOSCYTINA KANSASENSIS Tillyard

Permoscytina kansasensis Tillyard, 1926, Amer. J. Sci. 11: 388 (Lower Permian, Kansas).

Permoscytina kansasensis Tillyard, Carpenter, 1931, Amer. J. Sci. 22: 117.

Permoscytina kansasensis Tillyard, Carpenter, 1939, Proc. Amer. Acad. Arts Sci. 73: 49.

ARCHESCYTINA SOJANENSIS (Martynov)

Permoscytina sojanensis Martynov, 1933, Bull. Acad. Sci. U.R.S.S., Class. Sci. Math. et Nat., p. 884 (Permian, Russia).

Archescytina sojanensis (Martynov) Carpenter, 1939, Proc. Amer. Acad. Arts Sci. 73: 53.

PERMOPSYLLOPSIS ROSSICA Zalessky

Permopsyllopsis rossica Zalessky, 1939, Probl. Paleont., Moscow 5: 38 (Permian, Russia).

PERMOSCYTINOPSIS MAUERIAEFORMIS Zalessky

Permoscytinopsis maueriaeformis Zalesskey, 1939, Probl. Paleont., Moscow 5: 36 (Permian, Russia).

The specimen on which this species is based is almost complete. The antenna is long and has about 15 segments and the basal part of the apical abdominal process is preserved. While the venation is basically identical with that of Figure 1*B*, it differs in having an additional cross-vein linking *Rs* and *M*, and the 3 branches of *M* are shorter in relation to *R* and its branches than is the case with other archescytinids. A similar development of *M* occurs in certain of the Scytinopteridae.

SCYTONEURELLA MAJOR Zalessky

Scytoneurella major Zalessky, 1939, Probl. Paleont., Moscow 5: 39 (Permian, Russia).

This species was placed by Zalessky in the family Cicadopsyllidae. It resembles the wing illustrated in Figure 1*B*, but the 3 branches of *M* are relatively shorter.

SCYTONEURELLA MINOR Zalessky

Scytoneurella minor Zalessky, 1939, Probl. Paleont., Moscow 5: 39 (Permian, Russia).

SOJANOSCYTINA LATIPENNIS Martynov

Fig. 1*E*

Sojanoscytina latipennis Martynov, 1933, Bull. Acad. Sci. U.R.S.S., Class. Sci. Math. et Nat., p. 887 (Permian, Russia).

Martynov regarded this as a hindwing. Since Kansas representatives of the Archescytinidae have almost identical fore- and hindwings, Carpenter (1939) considered this to be the wing of an insect not belonging to this family. The proximal crossvein *r-m* is homologous with one in a similar position in *Permoscytinopsis maueriaeformis* and occurs also in the wing illustrated in Figure 1*G* (*S. grandis*). The forked condition of *Rs* is without special significance. Martynov's opinion that this wing is the hindwing of an archescytinid is supported.

SOJANOSCYTINA GRANDIS Martynov

Fig. 1*G*

Sojanoscytina grandis Martynov, 1933, Bull. Acad. Sci. U.R.S.S., Class. Sci. Math. et Nat., p. 886 (Permian, Russia).

Although this wing has anomalous venation, since M_2 is forked, it is of particular interest because of its resemblance to the wing of *S. latipennis* in three particulars. These are: the development of 2 crossveins between *Rs* and *M*; the basal angle of Cu_1 is approximately a right angle; the tendency (fully realized in *S. latipennis*) for a *Y*-vein to be developed in the clavus. It is in fact quite possible that Figures 1*G* and 1*E* represent the fore- and hindwings of a representative of the same species.

SOJANOSCYTINA MINOR Martynov

Sojanoscytina minor Martynov, 1933, Bull. Acad. Sci. U.R.S.S., Class. Sci. Math. et Nat., p. 887 (Permian, Russia).

In this wing M_4 is forked. Otherwise, except for the fact that it has a normal Cu_1 with 2 branches, it resembles in essentials the wing illustrated in Figure 1*A*.

PALEOSCYTINA BREVISTIGMA Carpenter

Fig. 1*H*

Paleoscytina brevistigma Carpenter, 1931, Amer. J. Sci. 22: 118 (Lower Permian, Kansas).

Carpenter regarded this wing as having Cu_1 with a single branch, and stated, though with doubtful reason, that such a reduction of Cu_1 occurs in many recent cicadellids. Cu_1 is, however, a particularly stable vein and though it may sometimes have an additional branch (e.g. Fig. 1*A*), unlike *M*, it is seldom reduced. My own interpretation of the venation of this wing is that both *M* and Cu_1 have 2 branches.

LITHOSCYTINA CUBITALIS Carpenter

Lithoscytina cubitalis Carpenter, 1933, Proc. Amer. Acad. Arts Sci. 68: 436 (Lower Permian, Kansas).

The apices of *Rs*, *M*, and Cu_1 are not preserved. On the strength of the fact that Cu_1 is not arched basally towards *M*, Carpenter created a family, the Lithoscytinidae, for the reception of this genus. He regarded the wing as that of the most primitive homopteron yet found. It is certain that the insect must have had weak powers of flight.

AUSTROSCYTINA IMPERFECTA Evans

Fig. 1*I*

Austroscytina imperfecta Evans, 1943, Rec. Aust. Mus. **21**: 180 (Upper Permian, New South Wales).

If this hindwing is correctly ascribed to the Archescytinidae, and this is by no means certain, it is the sole representative of this family to have been, so far, recorded from Australia. It resembles the forewing of *L. cubitalis* in having Cu_1 not associated with *M* proximally.

URALOSCYTINA PROSBOLOIDES Zalessky

Fig. 1*D*

Uraloscytina prosboloides Zalessky, 1939, Probl. Paleont., Moscow **5**: 40 (Permian, Russia).

Although *Rs* is forked and *M* is anomalous these features do not seem to provide justification for a separate family, as proposed by Zalessky.

URALOSCYTINA SIMILIS Zalessky

Uraloscytina similis Zalessky, 1939, Probl. Paleont., Moscow **5**: 40 (Permian, Russia).

This wing is similar in venation to that of *U. prosboloides* but smaller in size.

MAUERIA SYLVENSIS Zalessky

Maueria sylvensis Zalessky, 1939, Probl. Paleont., Moscow **5**: 41 (Permian, Russia).

Zalessky created a new family, the Maueridae, and a new order, the Hemipsocoptera for the reception of this and the wing of the following species. Carpenter (1939) has pointed out that this insect is a typical archescytinid. Neither of the 2 wings of the specimen, on which the description is based, is well preserved.

MARIPSOCUS AMBIGUUS Zalessky

Maripsocus ambiguus Zalessky, 1939, Probl. Paleont., Moscow **5**: 44 (Permian, Russia).

This wing was also placed by Zalessky in his order Hemipsocoptera, but in a separate family, the Maripsocidae. The state of preservation of the figured specimen is poor.

ARCHEGLYPHIS CRASSINERVIS Martynov

Fig. 1*F*

Archeglyphis crassinervis Martynov, 1930, Trans. Geol. Prosp. Serv. U.S.S.R. **49**: 99 (Upper Carboniferous, Russia).

Martynov regarded this as the wing of a prosbolid. It is certainly not a prosbolid and may in fact be the wing of an insect belonging to another order. It is included, tentatively, in the Archescytinidae because of its resemblance in certain anomalous features with the wing of *U. prosboloides* (Fig. 1*D*).

Discussion of the Archescytinidae

Martynov (1933), regarded representatives of this family as archaic Sternorrhyncha, related especially to the Aphididae. His reasons were that the forewings were membranous, the antennae long and many-segmented, and the hindwings not expanded in the anal area. He dismissed the fact that the insects have 3-segmented tarsi, which are not found among the Sternorrhyncha, as an archaic feature of no significance.

It has already been mentioned that Carpenter (1939), who interpreted the long apical abdominal process of the Archescytinidae as a respiratory tube, was of the opinion that the family was one which could not be ancestral to any groups of recent Homoptera.

It is possible that the Archescytinidae may be ancestral both to the Scytinopteridae and the Prosbolidae. If this is so, then they may lie on the direct line of descent of the whole of the Cicadomorpha (Evans 1951).

I have earlier given one reason why I consider that recognition of a separate division, the Paleorrhyncha, to comprise the Archescytinidae, is unnecessary. Others are: the venation of their wings has no features which differ from those of the basic type of venation of the forewings of insects in the cicadelloid complex (Evans 1946*a*, 1948); the possession of membranous wings is a characteristic shared with many recent leaf-hoppers (e.g. *Nicomia cicadoides* Walker, *Stenoscopus drummondi* Evans); many cicadellids have long antennae and some have the appearance of being multi-segmented (e.g. *Ciccus latreilli* Distant, *Neocoelidia fuscodorsata* Walker, *Occinirrana eborea* Evans); cicadelloids have 3-segmented tarsi.

Archescytinids differ from psylloids as they have larger wings and less specialized venation.

Formerly (Evans 1948) I have suggested that the Archescytinidae could be regarded as a family of the Cicadelloidea. My views as to their close relationship with this superfamily remain the same as before. However, as in the retention of a complete tentorium, cercopids and cicadas retain a feature absent in the heads of leaf-hoppers, it is preferable to regard the family Archescytinidae as separate and distinct from the Cicadelloidea.

Scytinopteridae, Prosbolidae (in part), and Related Families

If one were to remove the wings of representatives of a wide selection of recent Cicadelloidea and seek to determine their relationships with each other, it would be found possible, in most instances, to select family groups correctly. With a few, but not with many wings, subfamily and tribal affinities could also be determined.

The same degree of determination should be possible also with the wings of insects which are assembled from the strata of any particular geological period, though with these there must always be a risk of ascribing importance to features which might not be of much significance if other characteristics of the insects were also known.

The nodal line (Figs. 10*A-J*) may be such an unreliable feature for, while some leaf-hoppers having wings in which this line of weakness is developed have undoubtedly followed a separate line of evolutionary development from those lacking it, its presence in others may not necessarily be an indication of close genetic affinity.

For the purpose of this study two basic forms of forewings of Upper Permian Homoptera are recognized. These have identical venation, but with one, due to the presence of a nodal line, the apex of the wing is apically flexible in a downward direction. The two forms are illustrated in Figures 2*A* and 10*A*. A nodal line, as illustrated in Figure 10*A*, is homologous with the similar transverse line of weakness found in all recent cicadas. It is developed also in one recent family of leaf-hoppers, the Hylicidae.

The possession of an apically flexible forewing is clearly of benefit for flight purposes. This doubtless is the reason why a nodal line has remained a persistent feature over such a long period of time.

Upper Permian and Triassic Homoptera which lack a nodal line and have either basic venation, reduced venation, or specialized venation by way of the development of accessory veins, are regarded as belonging to the family Scytinopteridae. Those related forms which have a transverse nodal line are regarded as prosbolids. Formerly the insects which comprise these two families have been grouped in the following ones: Scytinopteridae Handlirsch; Prosbolidae Handlirsch; Prosbolopsidae Martynov; Sojanoneuridae Bekker-Migdisova; Cicadopsyllidae Martynov; Pereboridae Zalessky; Permoglyphidae Evans; Cicadellidae Latreille. The family Coleoscytidae Martynov is retained and a new family, the Hylicellidae, is created. Both of these are derivatives of the Scytinopteridae but have a venational pattern of a particularly specialized nature.

Family **SCYTINOPTERIDAE** Handlirsch

Martynov (1928) drew attention to the fact that the limits of this family had not been determined and Bekker-Migdisova (1948) restricted it to comprise species in the genus *Scytinoptera* Handlirsch. These have a reduced venation and form only a small part of the family unit as here understood.

The basic type of venation of the forewings of the Scytinopteridae is illustrated in Figures 2*A-F*. As no entire hindwing with complete venation appears to have been recorded, reference needs to be made to Figure 10*K* which illustrates the venation of the hindwing of a prosbolid. Doubtless the basic type of hindwing venation will have been identical in the two families.

The generalized venational pattern of the Scytinopteridae is very similar to that of the Archescytinidae. The principal differences are the incorporation of *Sc* in the costal margin of the tegmina of scytinopterids, and the change in the shape of the hindwing. The difference in the shape of the costal margin of the hindwing is associated with the development of a wing-coupling apparatus. The relative increase of the area of the wing posterior to Cu_2 and the acquisition of folds are doubtless changes which have accompanied flight by wings moving in unison instead of separately.

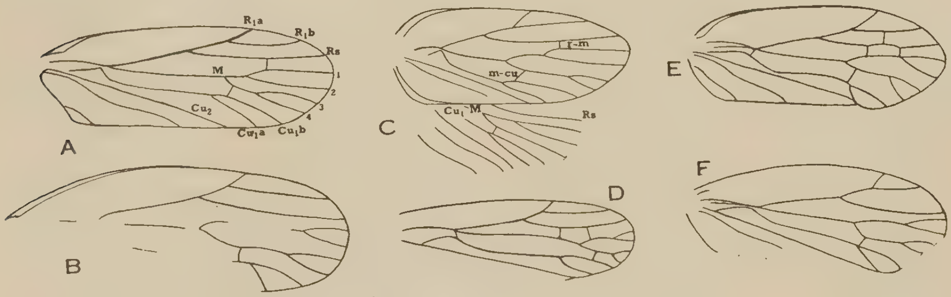

Fig. 2.—*A, Permocicadopsis angustata; B, Triassoscytina incompleta; C, Permocicada integra; D, Stenoscytina australiensis; E, Homaloscytina plana; F, Permojassus australis.*

Generalized Forms

PERMOCICADOPSIS ANGUSTATA (Martynov)

Fig. 2*A*

Permocicada angustata Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 4: 15 (Permian, Russia).

Permocicadopsis angustata (Martynov) Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 56.

Bekker-Migdisova figured and named 5 separate venational types which she associated with this specific name, which, following Martynov, she placed in the Prosbolidae. As well as numerous tegmina, other parts of the body have been preserved. These include the head, thorax, and apex of the abdomen. The head, apart from the development of a wide crown and the presence of a median ocellus, does not differ appreciably from those of recent aetalionids. The prothorax would seem to bear lateral paranota. The abdomen lacks an apical prolongation.

PERMOCICADOPSIS INSIGNIS (Martynov)

Permocicada sp. 1 Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 4: 15 (Permian, Russia).

Permocicadopsis insignis (Martynov), Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 64.

The venation of the tegmen figured by Bekker-Migdisova differs from that of *P. angustata* in having M_3 and M_4 apically shorter than M_1 and M_2. In Martynov's illustration, *M* is anomalous, since a 5th branch is shown but this may be due to misinterpretation of the fossil.

PERMOCICADOPSIS LEPTOPALENSIS Bekker-Migdisova

Permocicadopsis leptopalensis Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 56 (Permian, Russia).

The venation of this tegmen is similar to that illustrated in Figure 2*A*.

PERMOCICADA INTEGRA Bekker-Migdisova

Fig. 2*C*

Permocicada integra Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 32 (Permian, Russia).

Bekker-Migdisova placed the genus *Permocicada* Martynov in the Prosbolidae. As well as the tegmen, part of the hindwing is also shown in Figure 2*C*. It will be noted that $M_3 + M_4$ form a single vein and the same development of *M* is shown in an illustration of a complete hindwing given by Bekker-Migdisova. As well as the wings of this species, Bekker-Migdisova has figured also the head and the legs. It is of interest that the antennae are short and do not extend beyond the margin of the head.

The seven species listed below, although having tegmina of different shapes and proportions all resemble, in essential venational features, those illustrated in Figures 2*A* and 2*C*.

PERMOCICADA IDELENSIS Zalessky

Permocicada idelensis Zalessky, 1929, Trav. Soc. Nat. Univ. Kasan 52: 24 (Permian, Russia).

Permocicada idelensis Zalessky, Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 37.

PERMOCICADA NIGRONERVOSA Martynov

Permocicada nigronervosa Martynov, 1928, Trav. Mus. Geol. U.R.S.S. 4: 21 (Permian, Russia).

Permocicada nigronervosa Martynov, Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 39.

PERMOCICADA PERLATA Bekker-Migdisova

Permocicada perlata Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 41 (Permian, Russia).

PERMOCICADA SUBLATA Bekker-Migdisova

Permocicada sublata Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 40 (Permian, Russia).

PERMOCICADA SIMILIS Zalessky

Permocicada similis Zalessky, 1929, Trav. Soc. Nat. Univ. Kasan 52: 25 (Permian, Russia).

PERMOCICADA SUBTRUNCATA Martynov

Permocicada subtruncata Martynov, 1935, Trav. Inst. Paléozool. U.R.S.S. 4: 14 (Permian, Russia).

PROSBOLE OVALIS Martynov

Prosbole ovalis Martynov, 1935, Trav. Inst. Paléozool. U.R.S.S. 4: 6 (Permian, Russia).

The four following species are based on wings recorded from the Upper Permian of Australia:

HOMALOSCYTINA PLANA Tillyard

Fig. 2*E*

Homaloscytina plana Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 16 (Upper Permian, New South Wales).

Homaloscytina plana Tillyard, Evans, 1943, Rec. Aust. Mus. 21: 185.

The genus *Homaloscytina* Tillyard was placed by the author in the Scytinopteridae. Previously I have figured 10 tegmina, no two of which were identical, which I ascribed to this species. The only significant difference between the venation of *H. plana* and that of *P. angustata* (Fig. 2*A*) is the presence in the former of 2 crossveins which do not occur in the Russian species.

PERMOJASSUS AUSTRALIS Tillyard

Figs. 2*F*, 3*N*

Permojassus australis Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 7 (Upper Permian, New South Wales).

Tillyard illustrated both a fore- and a hindwing of this insect, which he placed in the Scytinopteridae. While his figure of the tegmen presents no particularly unusual features, that of the hindwing resembles no known wing of a homopteron. Accordingly a search has been made for the type specimens. These were found in the Australian Museum, and the figures listed above have been drawn from them and are not reproductions from Tillyard's illustrations. The venation of the tegmen is similar to that of the basic scytinopterid type. The wing is of particular interest as the costal margin is convexly rounded and there is a wide intercostal space. These features suggest that it represents an earlier evolutionary development than that of other known hindwings of scytinopterids and prosbolids.

STENOSCYTINA AUSTRALIENSIS Tillyard

Fig. 2*D*

Stenoscytina australiensis Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 15 (Upper Permian, New South Wales).

Genus TRIASSOSCYTINA, gen. nov.

Homoptera from the Upper Triassic of Queensland having tegmina with complete venation which differ from those of *Homaloscytina* in having the proximal point of separation of M into M_{1+2} and M_{3+4} lying immediately below the commencement of Rs and not in a more distal position.

Type species *Triassoscytina incompleta,* sp. nov.

TRIASSOSCYTINA INCOMPLETA, sp. nov.

Fig. 2*B*

Length of tegmen 10.8 mm; greatest width 4 mm. Holotype tegmen C1559, Department of Geology Collection, University of Queensland, from Mount Crosby, Queensland (Upper Triassic). This poorly-preserved wing is figured and named because of its interest in being the first scytinopterid recorded from Upper Triassic strata to retain a complete basic venational pattern.

Scytinopterids with Reduced Venation

PERMOCICADA BOREALIS Martynov

Fig. 3*A*

Permocicada borealis Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 4: 13 (Permian, Russia).

Permocicada borealis Martynov, Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 38.

Both Martynov and Bekker-Migdisova placed this tegmen in the Prosbolidae. It is here considered with the Scytinopteridae because there is doubt whether the faint transverse impression, recorded as a broken line in the figure, is an indication of the presence of a nodal line. It is grouped with the other tegmina illustrated in Figure 3, even though it is closer to those in Figure 2, because M_{1+2} form a single vein. The apical forking of M_4 is of no significance.

SOJANONEURA INNOMINATA Bekker-Migdisova

Fig. 3*B*

Sojanoneura bimaculata Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 4: 7 (Permian, Russia).

Sojanoneura innominata Bekker-Migdisova (nom. nov.), 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 52.

The genus *Sojanoneura* Martynov was placed in the Prosbolidae both by Martynov and Bekker-Migdisova. The reduction of venation brought about by M_{3+4} being represented by a single vein is of common occurrence in the Scytinopteridae and parallels a similar development within the Archescytinidae.

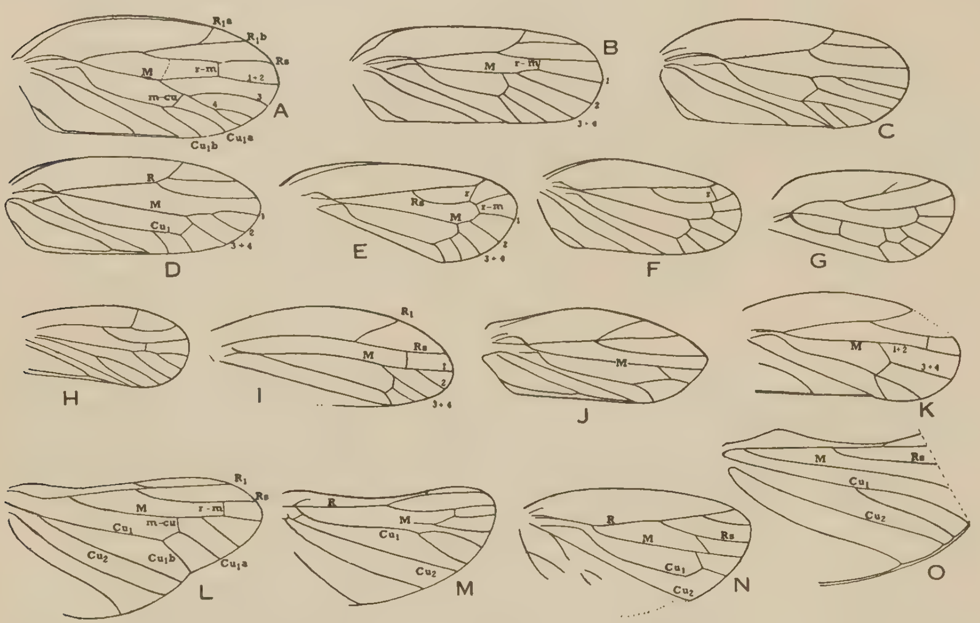

Fig. 3.—*A*, *Permocicada borealis;* *B*, *Sojanoneura innominata;* *C*, *S. elytrata;* *D*, *Scytinoptera reducta;* *E*, *S. kokeni;* *F*, *S. maculata;* *G*, *S. signata;* *H*, *Scytocixius mendax;* *I*, *Scytinoptera mexicana;* *J*, *S. cubitalis;* *K*, *Permojassus dubius;* *L*, *Scytinoptera reducta;* *M*, *Anomaloscytina metapteryx;* *N*, *Permojassus australis;* *O*, *Mesojassula marginata.*

SOJANONEURA TINCTA Bekker-Migdisova

Sojanoneura tincta Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 47.

The venation of this tegmen differs from that of *S. innominata* only in lacking *r-m* and in the relative proportions of the parts of *M*.

SOJANONEURA TRIANGULARIS Martynov

Sojanoneura triangularis Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 4: 9 (Permian, Russia).

Sojanoneura triangularis Martynov, Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 47.

Martynov's illustration of this tegmen resembles Figure 3*B* in essential features. It differs in having *r-m* in alignment with the base of *Rs* and M_4. Bekker-Migdisova has figured a tegmen, and listed several others besides, in which *r-m* is as shown in Figure 3*B* and there is also an additional sloping crossvein extending from the point of separation of R and Rs to the common stalk of M_1 and M_2. Furthermore in her illustration, M_3 and M_4 are present as separate veins.

SOJANONEURA DUBIOSA Martynov

Sojanoneura dubiosa Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 4: 8 (Permian, Russia).

Sojanoneura dubiosa Martynov, Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 51.

The venation resembles that of the wing illustrated in Figure 3*B*.

SOJANONEURA ELYTRATA Martynov

Fig. 3*C*

Sojanoneura elytrata Martynov, 1928, Trav. Mus. Geol. U.R.S.S. 4: 25 (Permian, Russia).

Sojanoneura elytrata Martynov, Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 51.

The separation of Cu_1 into 2 veins is of no special significance.

PERMOCICADA ELLIPTICA (Martynov)

Scytoneura elliptica Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 4: 16 (Permian, Russia).

Permocicada elliptica (Martynov), Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 42.

This tegmen, which Martynov placed in the Cicadopsyllidae, resembles the one illustrated in Figure 3*B* except for the fact that the arms of Cu_1 are longer than M and *m-cu* is differently situated.

CICADOPSYLLA PERMIANA Martynov

Cicadopsylla permiana Martynov, 1930, Trav. Mus. Geol. U.R.S.S. 8: 173 (Permian, Russia).

Cicadopsylla permiana Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 4: 16.

This tegmen, which like the above was included by Martynov in his family the Cicadopsyllidae, is similar in venation, though different in proportions to the one illustrated in Figure 3*B*.

PERMOCICADOPSIS ABERRANS (Martynov)

Sojanoneura aberrans Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 4: 9. (Permian, Russia).

Permocicadopsis aberrans (Martynov), Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 63.

This species has formerly been regarded as a prosbolid. Martynov mentions that the nodal line is indistinct and in the figure of a tegmen which Bekker-Migdisova ascribes to this species, it is not shown at all.

It is for this reason that it is included in the Scytinopteridae. The venation of the tegmen resembles Figure 2*B*.

SCYTINOPTERA REDUCTA (Martynov)

Figs. 3*D*, 3*L*

Anomoscyta reducta Martynov, 1928, Trav. Mus. Geol. U.R.S.S. 4: 34 (Permian, Russia).

Scytinoptera reducta (Martynov), Bekker-Migdisova, 1948, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 15: 16.

Scytinoptera ivensis Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 4: 22.

Scytinoptera ivensis Martynov, Bekker-Migdisova, 1948, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 15: 16.

Although Martynov records that the state of preservation of the holotype tegmen is "fine", his figure suggests otherwise. Bekker-Migdisova gives illustrations of several tegmina and wings which she ascribes to this species and Figures 3*D* and 3*L* have been copied from her paper. This species is listed before *S. kokeni*, the type of the genus, because in the tegmen of the former R_1a is retained and an additional r is lacking. Furthermore, although the 3 branches of M are considerably shorter than those of previously-listed forms, they are nevertheless not so greatly reduced as they are in the type species. The reduction in the venation of the wing has proceeded further than that of the tegmen since in the former M has only 2 branches.

PERMOCICADA TRIRAMOSA Bekker-Migdisova

Permocicada triramosa Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 40 (Permian, Russia).

The venation is similar to that of *S. reducta*.

SCYTINOPTERA KOKENI Handlirsch

Fig. 3*E*

Scytinoptera kokeni Handlirsch, 1904, Mém. Acad. Sci. St-Pétersb. 16: 3 (Permian, Russia).

Scytinoptera kokeni Handlirsch, 1908, Die Fossilen Insekten, p. 392.

Scytinoptera kokeni Handlirsch, Martynov, 1928, Trav. Mus. Geol. U.R.S.S. 4: 29.

Scytinoptera kokeni Handlirsch, Bekker-Migdisova, 1948, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 15: 8.

This tegmen is characterized by the loss of R_1a, the presence of r, and the short apical branches of M and Cu_1. A different interpretation of the venation has been proposed by Heslop-Harrison (1955*a*, 1955*b*) who regards crossvein r and M_1 as representing R_{2+3} and R_{4+5} respectively. However, in its basic development the radial sector of Homoptera is almost certainly a single vein. Bekker-Migdisova has figured the abdomen and the male genitalia of this species.

SCYTINOPTERA MACULATA Martynov

Fig. 3*F*

Scytinoptera maculata Martynov, 1928, Trav. Mus. Geol. U.R.S.S. 4: 31 (Permian, Russia).

Scytinoptera maculata Martynov, Bekker-Migdisova, 1948, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 15: 14.

This tegmen is very similar to the preceding one and differs principally in shape and in the position of *r*.

SCYTINOPTERA CURTA Zalessky

Scytinoptera curta Zalessky, 1929, Trav. Soc. Nat. Univ. Kasan 52: 28 (Permian, Russia).

Scytinoptera curta Zalessky, Bekker-Migdisova, 1948, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 15: 13.

A tegmen which closely resembles that of *S. maculata*.

SCYTINOPTERA SIGNATA Martynov

Fig. 3*G*

Scytinoptera signata Martynov, 1930, Trav. Mus. Geol. U.R.S.S. 8: 172 (Permian, Russia).

Scytinoptera signata Martynov, Bekker-Migdisova, 1948, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 15: 16.

This tegmen has a somewhat more specialized venation than those illustrated in Figures 3*E* and 3*F*. A comparison of the tegmina illustrated in Figures 3*D-G*, provides an example of the difficulty of deciding on specific and generic placings when wings only are available for study. Thus these 4 tegmina could be regarded as those of four species in one genus, two genera (Fig. 3*D* and Figs. 3*E-G*), or even three (Fig. 3*D*, Figs. 3*E* and 3*F*, Fig. 3*G*) might be recognized.

SCYTINOPTERA CUBITALIS Bekker-Migdisova

Fig. 3*J*

Scytinoptera cubitalis Bekker-Migdisova, 1948, Trav. Inst. Paléozool. Acad. Sci. U.R.R.S. 15: 27 (Permian, Russia).

This tegmen differs in several venational features from those of other tegmina of insects in the genus *Scytinoptera*. Thus R_1a is retained, *r-m* is lacking, and *M* is reduced to a single vein. There is a *Y*-vein in the clavus, as in *S. reducta*, but not in *S. maculata*. A reduction to 4 in the number of the veins supporting the apex of the tegmen is a development which occurs also in recent families belonging to the Cicadelloidea. In addition to tegmina, Bekker-Migdisova has figured the head and thorax of this insect in both dorsal and lateral aspects. The head resembles that of an aetalionid (Evans 1946) ; but it differs in having a median ocellus and a wide crown. The pronotum would appear to have lateral paranota.

SCYTINOPTERA OBLIQUO-OVATA Martynov

Scytinoptera obliquo-ovata Martynov, 1928, Trav. Mus. Geol. U.R.R.S. **4**: 32 (Permian, Russia).

Scytinoptera similis Martynov, 1928, Trav. Mus. Geol. U.R.R.S. **4**: 33.

Scytinoptera obliquo-ovata Martynov, Bekker-Migdisova, 1948, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. **15**: 15.

This tegmen closely resembles those of *S. kokeni* and *S. maculata* (Figs. 3*E*, 3*F*), except for the fact that a *Y*-vein is developed in the clavus.

PERMOJASSUS DUBIUS Tillyard

Fig. 3*K*

Permojassus dubius Tillyard, 1926, Proc. Linn. Soc. N.S.W. **51**: 8 (Upper Permian, New South Wales).

This tegmen, which has not been figured previously, is of interest as another example from the Permian of one in which the veins reaching to the apex of the tegmen are reduced to 4 in number. The type specimen is in the Australian Museum.

SCYTINOPTERA MEXICANA Carpenter & Miller

Fig. 3*I*

Scytinoptera mexicana Carpenter & Miller, 1937, Amer. J. Sci. **34**: 125 (Permian, Mexico).

This tegmen represents one of the two Permian Homoptera so far recorded from South America.

SCYTOCIXIUS MENDAX Martynov

Fig. 3*H*

Scytocixius mendax Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. **7**: 35 (Permian, Russia).

Martynov regarded this tegmen as being that of a cixiid. While the presence of a *Y*-vein in the clavus and the long arms of Cu_1 certainly suggest fulgoroid affinities, the venation is essentially that of a scytinopterid.

Scytinopterids with Accessory Veins

PERMOCIXIUS KAZANENSIS Martynov

Permocixius kazanensis Martynov, 1928, Trav. Mus. Geol. U.R.S.S. **4**: 36 (Permian, Russia).

This tegmen also was considered by Martynov as that of a cixiid. The venation is, however, of the basic scytinopterid type excepting that *M* has 3 branches. It is grouped here because of the anomalous condition of *Rs*, which is apically forked.

ELLIPTOSCARTA OVALIS Tillyard

Elliptoscarta ovalis Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 17 (Upper Permian, New South Wales).

This tegmen has complete venation and M_2 and Cu_1 are both forked.

Genus ORTHOSCYTINA

Tillyard (1926*b*) described and gave nine separate specific names to tegmina belonging to insects in this genus. All could equally have been regarded as representatives of a single species. In 1943 I figured, but did not name, 10 more tegmina and pointed out that exact correspondence could be found between none of these and those illustrated by Tillyard. Apart from the shape of the tegmen, the principal features characteristic of this genus are the development of numerous accessory veins associated with R_1 and Cu_1.

Type species *Orthoscytina mitchelli* Tillyard.

ORTHOSCYTINA MITCHELLI Tillyard

Fig. 4*A*

Orthoscytina mitchelli Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 10 (Upper Permian, New South Wales).

In Tillyard's figure a possible crossvein between R_1 and *Rs* is indicated by a dotted line. This has been omitted in Figure 4*A* since such a development occurs in no other tegmina of *Orthoscytina* spp.

ORTHOSCYTINA QUINQUEMEDIA Tillyard

Orthoscytina quinquemedia Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 11 (Upper Permian, New South Wales).

This tegmen differs from that of the type species in having M_4 forked and Cu_1 with 2 instead of 4 branches.

ORTHOSCYTINA INDISTINCTA Tillyard

Fig. 4*B*

Orthoscytina indistincta Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 11 (Upper Permian, New South Wales).

This is one of the 2 figured tegmina in which *M* is reduced.

ORTHOSCYTINA SUBCOSTALIS Tillyard

Orthoscytina subcostalis Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 11 (Upper Permian, New South Wales).

This tegmen has complete basic venation without any development of accessory veins.

The tegmina of the remaining species, which are listed below, represent minor venational aberrations of no particular significance:

ORTHOSCYTINA IRREGULARIS Tillyard

Orthoscytina irregularis Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 12 (Upper Permian, New South Wales).

ORTHOSCYTINA BELMONTENSIS Tillyard

Orthoscytina belmontensis Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 13 (Upper Permian, New South Wales).

ORTHOSCYTINA OBLIQUA Tillyard

Orthoscytina obliqua Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 13 (Upper Permian, New South Wales).

ORTHOSCYTINA PINCOMBEI Tillyard

Orthoscytina pincombei Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 14 (Upper Permian, New South Wales).

ORTHSCYTINA TETRANEURA Tillyard

Orthoscytina tetraneura Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 15 (Upper Permian, New South Wales).

Of the 10 tegmina figured previously by myself one only merits comment. This tegmen has complete basic venation excepting that R_1 has 10 equal and parallel branches (specimen F40001, Australian Museum Collection).

PERMOGLYPHIS BELMONTENSIS Tillyard

Fig. 4*F*

Permoglyphis belmontensis Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 22 (Upper Permian, New South Wales).

Permoglyphis belmontensis Tillyard, Evans, 1943, Rec. Aust. Mus. 21: 183.

The accompanying figure is based not on Tillyard's illustration but on a re-examination of the type specimen.

Tillyard placed this species and genus in the family Prosbolidae and in his figure suggested the presence of a nodal line but I have failed to recognize such a development. Previously (Evans 1943) I have created a new family, the Permoglyphidae to comprise the following genera: *Permoglyphis* Tillyard, *Permodipthera* Tillyard, *Permobrachus* Evans. Further study discloses that the tegmina of species in these genera lack sufficient distinctive features in common which merit a family grouping.

PERMOBRACHUS MAGNUS Evans

Fig. 4*C*

Permobrachus magnus Evans, 1943, Rec. Aust. Mus. 21: 183 (Upper Permian, New South Wales).

As already mentioned, I have previously ascribed this species to the family Permoglyphidae which I am now discarding. The tegmen should be compared with that of *Permopibrocha ramosa* (Fig. 4*I*) which has a similar venational development.

PERMOBRACHUS DUBIA (Tillyard)

Permodipthera dubia Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 24 (Upper Permian, New South Wales).

Permobrachus dubia (Tillyard), Evans, 1943, Rec. Aust. Mus. 21: 183.

The specimen on which this species is based is poorly preserved and of no particular interest.

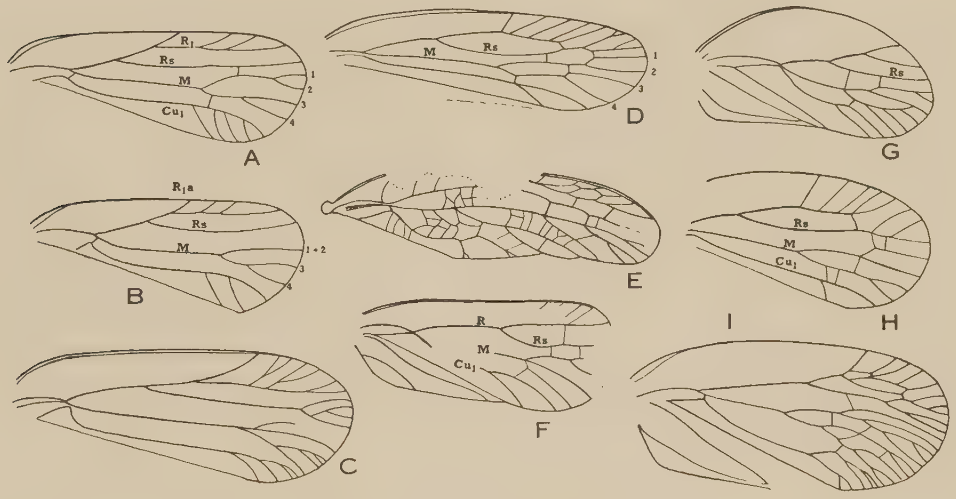

Fig. 4.—*A*, *Orthoscytina mitchelli*; *B*, *O. indistincta*; *C*, *Permobrachus magnus*; *D*, *Mesocixiella furcata*; *E*, *Stenoglyphis kimblensis*; *F*, *Permoglyphis belmontensis*; *G*, *Prosbolopsis ovalis*; *H*, *Mesocixiella asiatica*; *I*, *Permopibrocha ramosa*.

STENOGLYPHIS KIMBLENSIS Evans

Fig. 4*E*

Stenoglyphis kimblensis Evans, 1947, Rec. Aust. Mus. 21: 43 (Upper Permian, New South Wales).

This tegmen is of interest because of its size, being 36 mm long, and because the venation is reticulate.

PEREBORIA BELLA Zalessky

Pereboria bella Zalessky, 1930, Bull. Acad. Sci. U.R.S.S., Class. Sci. Physico-Math., p. 1021 (Permian, Russia).

This also is a large tegmen, the preserved portion being 47 mm in length. The venation is reticulate.

PERMOPIBROCHA RAMOSA Martynov

Fig. 4*I*

Permopibrocha ramosa Martynov, 1935, Trav. Inst. Paléozool. U.R.S.S. 4: 18 (Permian, Russia).

Although the tegmen of this species is only 13 mm long it was placed by Martynov in the family Pereboridae Zalessky.

SCYTOPHARA EXTENSA Martynov

Scytophara extensa Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 7: 37. (Permian, Russia).

This small wing (7.5 mm) was referred by Martynov to the Pereboridae, a family considered as ancestral to the Dictyopharidae. As mentioned by Martynov the venation resembles that of *P. ramosa.*

In 1935 Martynov described and figured the tegmina of two Homoptera which he placed in a new genus *Prosbolopsis,* family Prosbolopsidae, and he ascribed the family to the Fulgoroidea. He also figured the thorax and lower surface of a specimen. Bekker-Migdisova (1946) has illustrated additional tegmina of insects belonging to Martynov's species and also well-preserved whole insects. These have pronotal paranota. As pointed out by Bekker-Migdisova, these insects superficially resemble fulgoroids belonging to the family Issidae. Further possible affinities with the Fulgoroidea are suggested by the structure of their heads. Nevertheless, I am of the opinion that they are specialized scytinopterids and not fulgoroids.

PROSBOLOPSIS OVALIS Martynov

Fig. 4*G*

Prosbolopsis ovalis Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 14: 19 (Permian, Russia).

Prosbolopsis ovalis Martynov, Bekker-Migdisova, 1946, Bull. Acad. Sci. U.R.S.S., Biol. Ser., p. 757.

The special characteristic of this tegmen, apart from its shape and the wide costal space, is the distal position of the point of meeting of the 3 principal veins. In Figure 4*G*, which is taken from Martynov's illustration, *M* alone has accessory veins, but in tegmina figured by Bekker-Migdisova they are associated also with R_1.

PROSBOLOPSIS SIMPLEX Martynov

Prosbolopsis simplex Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 14: 20 (Permian, Russia).

The tegmen of this species differs in shape from that of the type species.

ANAPROSBOLE IVENSIS Bekker-Migdisova

Anaprosbole ivensis Bekker-Migdisova, 1946, Bull. Acad. Sci. U.R.S.S., Biol. Ser., p. 761 (Permian, Russia).

This genus was placed by Bekker-Migdisova in the Prosbolopsidae. The tegmen of *A. ivensis* resembles those of *Orthoscytina* spp. in venation, since both R_1 and Cu_1 have accessory veins, but it differs in shape. If the hindwing figured by Bekker-Migdisova belonged to the same insect as the forewing then it is doubtful whether it was able to fly.

MESODIPTHERA PROSBOLOIDES Tillyard

Mesodipthera prosboloides Tillyard, 1922, Proc. Linn. Soc. N.S.W. 47: 481 (Upper Triassic, Queensland).

Tillyard regarded this tegmen and the one following as having belonged to Trophiduchidae. I have examined the type specimen, which is in the Australian Museum, and found it difficult to interpret since it is confused by some of the veins of the underlying hindwing. It is, however, certainly not the tegmen of a fulgoroid but of a scytinopterid with accessory veins.

MESODIPTHERA DUNSTANI Tillyard

Mesodipthera dunstani Tillyard, 1922, Proc. Linn. Soc. N.S.W. 47: 462 (Upper Triassic, Queensland).

This tegmen, which is of an incomplete but better-preserved specimen than the foregoing, is also that of a scytinopterid with specialized venation. The type specimen has not been available for examination but it should be noted that the base of Cu_1 cannot possibly be as indicated in Tillyard's illustration. Furthermore, the apparent transverse vein indicated in the basal part of the costal area cannot be part of the structure of the wing.

The four species of *Mesocixiella* listed below are from a considerably more recent geological horizon. While they retain, to a large extent, venational features associated with tegmina recorded from earlier periods, it will be noted that the proximal bend of Cu_1 is less strongly developed.

MESOCIXIELLA ASIATICA Martynov

Fig. 4*H*

Mesocixiella asiatica Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 7: 89 (Lias, Russia).

Martynov placed this insect in the Cixiidae, but it is undoubtedly that of a scytinopterid with a slight development of accessory veins.

MESOCIXIELLA FURCATA Martynov

Fig. 4*D*

Mesocixiella furcata Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 7: 92 (Lias, Russia).

The venation of this tegmen resembles that of *M. asiatica* in having accessory veins associated only with *R* and *Rs*.

MESOCIXIELLA EXTENSA Martynov

Mesocixiella extensa Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 7: 90 (Lias, Russia).

This tegmen is similar to that of *M. furcata.* The principal difference is that M_4 is divided into 2 veins.

MESOCIXIELLA MAJOR Martynov

Mesocixiella major Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 7: 93 (Upper Lias, Russia).

The following 11 new species, which are placed in seven new genera, are scytinopterids which have tegmina with accessory veins developed. All are from Triassic strata in Australia, one being from beds of Brookvale Series in New South Wales (Middle Triassic) whilst the others are from the Mt. Crosby beds in Queensland (Upper Triassic).

Genus TRIASSOSCYTINOPSIS, gen. nov.

Homoptera having tegmina which are parallel-sided and evenly rounded apically. R_1 has 4 or more parallel-sided branches; *Rs* may be single or have 2 branches; *M* has a full complement of 4 branches and Cu_1 has normal venation and a sharp proximal bend. The anal veins are separated from each other for their entire length.

Type species *Triassoscytinopsis stenulata,* sp. nov.

The tegmina of *Triassoscytinopsis* spp. resembles those of *Orthoscytina* spp. in venational features but *R* is more nearly parallel with the costal margin.

TRIASSOSCYTINOPSIS STENULATA, sp. nov.

Fig. 5*C*

Length of tegmen 9 mm; greatest width 2 mm. R_1 with 4 branches. Holotype tegmen C917, Department of Geology Collection, University of Queensland, from Mt. Crosby, Queensland (Upper Triassic).

TRIASSOSCYTINOPSIS ABERRANS, sp. nov.

Fig. 5*J*

Length of tegmen 9.2 mm; greatest width 3 mm. Clavus rugose. Differs from the tegmen of the type species in having an additional branch of R_1 and in *Rs* being forked for approximately half its length. The base of the tegmen is unusually well preserved and also the scutellum. Holotype tegmen C1532, Department of Geology Collection, University of Queensland, from Mt. Crosby, Queensland (Upper Triassic).

TRIASSOSCYTINOPSIS PARANOTALIS, sp. nov.

Fig. 5*A*

Length of whole insect 21 mm, of tegmen 16 mm; greatest width of tegmen 6.8 mm. The pronotum has well-developed lateral paranota. *T. paranotalis* differs from the type species in having R_1 with 6 branches (though this number is apparently present only in one of the two tegmina) and in having a crossvein between R_1 and *Rs*. Holotype tegmen F38265, Australian Museum Collection, from Brookvale, New South Wales (Middle Triassic).

Genus MESOTHYMBRIS, gen. nov.

The tegmina of species in this genus resemble those of *Triassoscytinopsis* spp. in basic venational features. They differ in shape and in the characteristic shape of *M*. M_{1+2} form an almost continuous straight line with the basal part of the vein and M_{3+4} is sharply bent towards crossvein *m-cu*.

Type species *Mesothymbris perkinsi*, sp. nov.

MESOTHYMBRIS PERKINSI, sp. nov.

Fig. 5*D*

Length of fragment of tegmen 7 mm; greatest width 3 mm. The costal space is unusually wide; R_1 has 5 branches and, in addition to crossvein *m-cu,* others are present between *R* and *Rs* and *R* and *M*. Holotype tegmen C889, Department of Geology Collection, University of Queensland, from Mt. Crosby, Queensland (Upper Triassic). Other specimens as follows: counterpart of the holotype C890; C186 (counterpart C185), length 8.5 mm; C183 (counterpart C184), length 9 mm; C1457, length 7 mm.

MESOTHYMBRIS WOODWARDI, sp. nov.

Fig. 5*B*

Length of fragment of tegmen 8 mm; greatest width 3 mm. Differs from the type species in the shape of the tegmen, in having a narrower costal space, and in having R_1 with 4 branches and no crossveins apart from *m-cu*. Holotype tegmen C1669, Department of Geology Collection, University of Queensland, from Mt. Crosby, Queensland (Upper Triassic).

Genus MESONIRVANA, gen. nov.

The tegmen has R_1 with 4 branches, M_1 and M_2 of equal length and M_{3+4} as a single vein. Cu_1 lies in a straight line as far as crosssvein *m-cu* and the arms of Cu_1 are apically parallel with each other.

Type species *Mesonirvana abrupta*, sp. nov.

Mesonirvana resembles *Mesothymbris* in having R_1 with several branches but differs in the position of *m-cu* in relation to Cu_1 and in the reduced media.

MESONIRVANA ABRUPTA, sp. nov.

Fig. 5*E*

Length of fragment of tegmen 9 mm; greatest width 4.7 mm. The apical forking of M_1 is regarded as an anomalous condition hence it has not been mentioned in the generic definition. Holotype tegmen C1652, Department of Geology Collection, University of Queensland, from Mt. Crosby, Queensland (Upper Triassic).

Genus TRIASSOSCELIS, gen. nov.

Homoptera having tegmina with venation similar to that of *M. abrupta* and others illustrated in Figure 5 in that R_1 has several branches and *M* is complete but differing in the development of *Rs* which has 2 branches.

Type species *Triassoscelis anomala,* sp. nov.

TRIASSOSCELIS ANOMALA, sp. nov.

Fig. 5*F*

Length of fragment of tegmen 12 mm; greatest width 6 mm. R_1a, R_1b, and *Rs* all apically forked, *M* complete, and crossveins *r, r-m,* and *m-cu* are present. Holotype tegmen C976, Department of Geology Collection, University of Queensland, from Mt. Crosby, Queensland (Upper Triassic). Counterpart C977. Another specimen is illustrated in Figure 5*G* (C1881, Mt. Crosby; length of fragment 10 mm).

Genus CROSBELLA, gen. nov.

Homoptera from the Upper Triassic of Queensland which differ from related forms in having tegmina with numerous terminal accessory veins and, as well, supplementary crossveins.

Type species *Crosbella elongata,* sp. nov.

CROSBELLA ELONGATA, sp. nov.

Fig. 5*H*

Length of tegmen 12 mm; greatest width 6 mm. Surface with shallow pits. R_1, *Rs,* and *M* with accessory veins; 3 oblique veins between R_1 and *Rs* and 2 crossveins between *Rs* and *M*. M_1 a single vein, M_2 and M_3 with additional branches. Cu_1 not preserved. There may also be a series of short veins between *R* and the costal margin proximally of R_1, but the condition of the fossil makes their identity uncertain. Holotype tegmen

C2125, Department of Geology Collection, University of Queensland, from Mt. Crosby, Queensland (Upper Triassic).

CROSBELLA ALATA, sp. nov.

Fig. 5*K*

Length of fragment of tegmen 14 mm; greatest width 5.8 mm. Tegmen with widely-spaced punctures. Apical terminations of R_1 and *Rs* not preserved. *M* and Cu_1a with accessory terminal veins. As the apices only of some of the veins of the hindwing are exposed, certain interpretation is impossible. Holotype tegmen C174, Department of Geology Collection, University of Queensland, from Mt. Crosby, Queensland (Upper Triassic). Counterpart, C173, apex of wing only. Another specimen (hindwing in part) C1924.

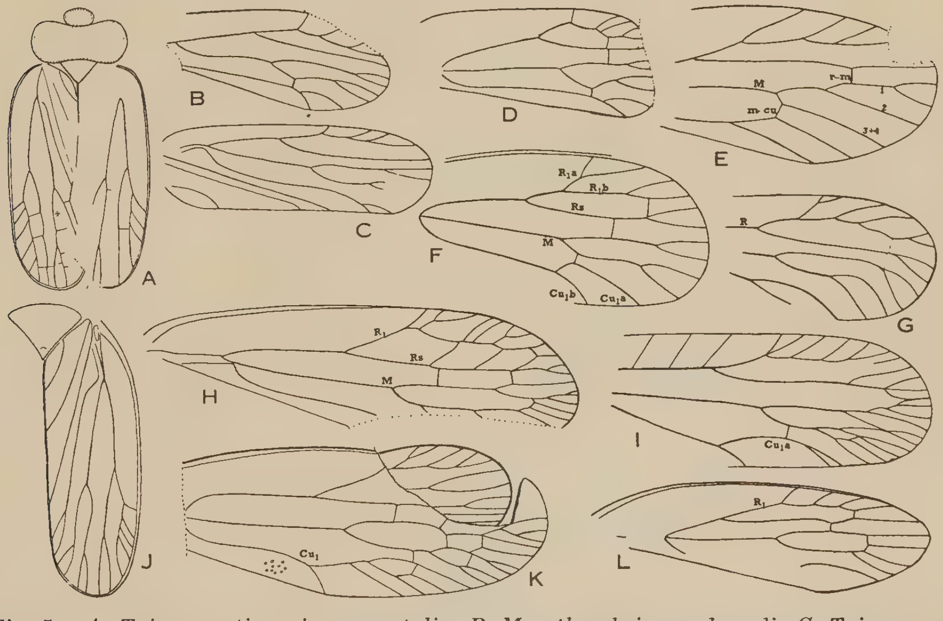

Fig. 5.—*A, Triassoscytinopsis paranotalis; B, Mesothymbris woodwardi; C, Triassoscytinopsis stenulata; D, Mesothymbris perkinsi; E, Mesonirvana abrupta; F, Triassoscelis anomala; G, T. anomala; H, Crosbella elongata; I, Mesocicadella venosa; J, Triassoscytinopsis aberrans; K, Crosbella alata; L, Triassocotis australis.*

Genus MESOCICADELLA, gen. nov.

Distinguished from other Triassic scytinopterids by the presence of a series of parallel oblique veins between *R* and the costal border proximally of the separation of *Rs* from R_1. R_1 and *Rs* with accessory veins, *M* profusely branched, and Cu_1a with an additional apical branch.

Type species *Mesocicadella venosa*, sp. nov.

MESOCICADELLA VENOSA, sp. nov.

Fig. 5*I*

Length of fragment of tegmen 12 mm; greatest width 5 mm. Holotype tegmen C844, Department of Geology Collection, University of Queensland, from Mt. Crosby, Queensland (Upper Triassic).

Genus TRIASSOCOTIS, gen. nov.

Upper Triassic Homoptera with long, narrow tegmina which narrow apically. R_1 with 4 branches, *Rs* single. *M* with 4 branches and with an enclosed cell between M_{1+2} and M_{3+4}. While the tegmen is different in shape and venational characteristics from those of other Triassic Homoptera, it has some resemblance to that of the Jurassic *Mesocixiella furcata* (Fig. 4*D*); also because of the cell enclosed by the arms of *M*, it has some resemblance to tegmina of species comprised in the Chiliocyclidae.

TRIASSOCOTIS AUSTRALIS, sp. nov.

Fig. 5*L*

Length of tegmen 11 mm; greatest width 3 mm. Holotype tegmen C1554, Department of Geology Collection, University of Queensland, from Mt. Crosby, Queensland (Upper Triassic). Counterpart C1553.

Specialized Forms

Three separate groups of genera are included under this subheading. All comprise species which have tegmina that differ appreciably in shape from those previously discussed, and have also a modified venational pattern.

Family **COLEOSCYTIDAE** Martynov

COLEOSCYTA ROTUNDATA Martynov

Fig. 6*A*

Coleoscyta rotundata Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 4: 24 (Permian, Russia).

This tegmen is of interest since, as happens also in recent cicadellids, *Rs* and *M* form a single vein for part of their length.

COLEOSCYTA VENOSA Martynov

Figs. 6*B*, 6*C*

Coleoscyta venosa Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. **4**: 25 (Permian, Russia).

The extent of the reduction of the venation of the hindwing is almost the same as that of the tegmen.

COLEOSCYTODES ELYTRATA Martynov

Coleoscytodes elytrata Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 4: 25 (Permian, Russia).

The venation of the tegmen is similar to that of *C. venosa.*

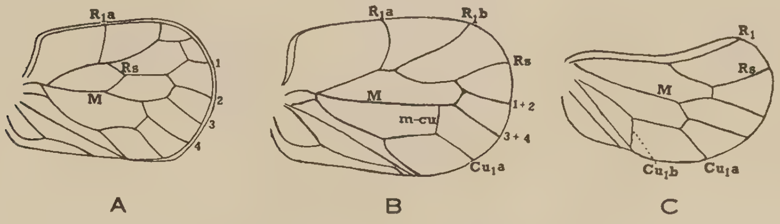

Fig. 6.—*A, Coleoscyta rotundata; B, Coleoscyta venosa* (tegmen); *C, C. venosa* (wing).

Family HYLICELLIDAE, fam. nov.

This family is created for the reception of Upper Triassic Homoptera with tegmina which resemble those of recent hylicids in having M_{3+4} in part incorporated in the same vein as Cu_1. They differ from hylicids in retaining Cu_1a and in having a more complete M. The wing impression of *Hylicella colorata*, sp. nov. has a possible nodal line but as its presence cannot be determined with certainty, it is omitted from Figure 7*A*.

Genus HYLICELLA, gen. nov.

Homoptera with tegmina in which M is either complete or reduced and with M_{3+4} in part incorporated with Cu_1a. Cu_1 with a steep basal bend. There are 2 crossveins between Rs and M and 1 between the arms of M.

Type species *Hylicella colorata*, sp. nov.

HYLICELLA COLORATA, sp. nov.

Fig. 7*A*

Length of tegmen 11 mm; greatest width 3.8 mm. A yellowish brown impression with 3 transverse black fasciae. R_1b terminates close to R_1a on the costal margin; in consequence R_1b is widely separated from Rs. M has 4 branches. Holotype tegmen C1841, Department of Geology

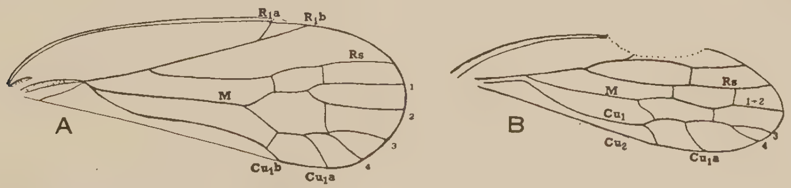

Fig. 7.—*A, Hylicella colorata; B, H. reducta.*

Collection, University of Queensland, Mt. Crosby, Queensland (Upper Triassic).

HYLICELLA REDUCTA, sp. nov.

Fig. 7*B*

Length of tegmen 8 mm; greatest width 3.5 mm. Differing from the type species in size and in the character of M_{1+2} forming a single vein. Holotype tegmen C1452, Department of Geology Collection, University of Queensland, Mt. Crosby, Queensland (Upper Triassic).

INCERTAE SEDIS

EOCHILIOCYCLA ANGUSTATA Davis

Fig. 8

Eochiliocycla angustata Davis, 1942, Proc. Linn. Soc. N.S.W. 67: 113 (Upper Permian, New South Wales).

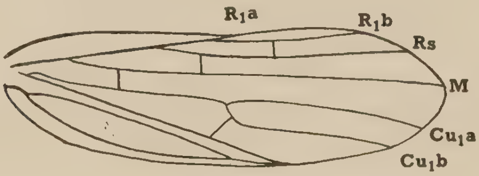

Fig. 8.—*Eochiliocycla angustata.*

Davis ascribed this tegmen tentatively to the Scytinopteridae and pointed out that it was very different from those of other known Permian Homoptera. The most unusual feature of the venation is the extension of the 2 branches of Cu_1 to the apex of the tegmen. Other unusual characteristics are the unbranched condition of *M* and the fact that Cu_1 is not proximally arched. The combination of a *Y*-vein in the clavus, Cu_1 with long arms, and Cu_1b not terminating close to the apex of the claval suture, suggest the possibility that this may be the forewing of a fulgoroid and not of an aberrant scytinopterid.

Family **PROSBOLIDAE** Handlirsch

Before discussing this family mention needs to be made of the family Protoprosbolidae Laurentiaux. This family is based on the forewing of an insect, *Protoprosbole straeleni* Laurentiaux (Fig. 9), from the Namurien (Carboniferous) of Belgium.

Laurentiaux (1953) has suggested that this wing may have belonged to an insect which was directly ancestral to the Prosbolidae and in particular to *Dictyoprosbole membranosa* and *Prosbole triangularis*, which in his opinion, are the most archaic prosbolids. Later, it will be shown that species in these two genera are the most highly specialized and not the most archaic representatives of the Prosbolidae. Moreover, the wing of *P. straeleni* has not a single feature which suggests homopterous affinities.

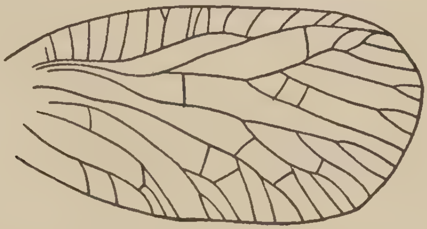

Fig. 9.—*Protoprosbole straeleni.*

If a comparison is made between the tegmen of *Prosbole reducta* (Fig. 10*A*) and those of *Permocicadopsis angustata* and *Homaloscytina plana* (Figs. 2*A*, 2*E*) it will be noted that the only significant difference between the 3 tegmina is the presence of a nodal division in the wing of *P. reducta.*

It has already been demonstrated how, in the Scytinopteridae, specialization took place by reduction of venation, by the acquirement of supplementary veins, and, in extreme cases, by the development of reticulate venation. Reference to Figures 10*A-G* will show how parallel specializations developed also in the Prosbolidae. In these figures the 6 top tegmina illustrated are of insects from the Permian of Russia, while *I* and *J* represent the wings of insects from the Permian of New South Wales.

It is clear that the two groups of wings belonged to insects which followed different lines of evolutionary development. The reason for the inclusion of the wings of Australian Homoptera within the Prosbolidae is that it is improbable that a nodal line became differentiated independently in Russia and Australia. Moreover, the close resemblance between the wings of Russian and Australian scytinopterids suggests that an interchange of fauna took place between the two regions during Permian times. There is some reason therefore for supposing that there was close genetic affinity between the two groups of insects ascribed to the Prosbolidae.

PROSBOLE REDUCTA Martynov

Figs. 10*A*, 10*D*

Prosbole reducta Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 4: 5 (Permian, Russia).

Prosbole reducta Martynov, Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 23.

Figure 10*A* is copied from Martynov's illustration and is of a tegmen with complete basic venation. Figure 10*C*, in which M_3 is forked, is from a figure given by Bekker-Migdisova.

PROSBOLE JUCUNDA Martynov

Prosbole jucunda Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. **4**: 3 (Permian, Russia).

Prosbole jucunda Martynov, Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. **11**: 23.

The venation of the tegmen of this species resembles that of *P. reducta.*

PROSBOLE INCERTA Bekker-Migdisova

Prosbole incerta Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. **11**: 25 (Permian, Russia).

The venation is, in part, obscure, but if Bekker-Migdisova's reconstruction is correct, it also resembles that of *P. reducta.*

SOJANONEURA SIGNATA Martynov

Sojanoneura signata Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. **4**: 10 (Permian, Russia).

Sojanoneura signata Martynov, Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. **11**: 51.

The principal feature in which this tegmen differs from that of *P. reducta* is the presence of a crossvein *m-cu* and the consequential change in the direction of the arms of Cu_1.

PERMOCICADA SIMULATRIX Martynov

Fig. 10*B*

Permocicada simulatrix Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. **4**: 14 (Permian, Russia).

Permocicada simulatrix Martynov, Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. **11**: 41.

Resembling *S. signata* in the possession of crossvein *m-cu* but differing from the basic type of venation in having M_3 and M_4 forming a single vein.

PERMOCICADA PUSILLA Bekker-Migdisova

Permocicada pusilla Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. **11**: 42 (Permian, Russia).

Similar venation to *P. simulatrix.*

SOJANONEURA EDEMSKII Martynov

Sojanoneura edemskii Martynov, 1928, Trav. Mus. Geol. U.R.S.S. **4**: 23 (Permian, Russia).

Sojanoneura edemskii Martynov, Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 48.

Similar venation to *P. simulatrix*.

SOJANONEURA KAZANENSIS Zalessky

Sojanoneura kazanensis Zalessky, 1929, Trav. Soc. Nat. Univ. Kasan 52: 26 (Permian, Russia).

Similar venation to *P. simulatrix*.

PROSBOLE PROPINQUA Bekker-Migdisova

Prosbole propinqua Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 25 (Permian, Russia).

An aberrant form in which M_{3+4} has an additional branch.

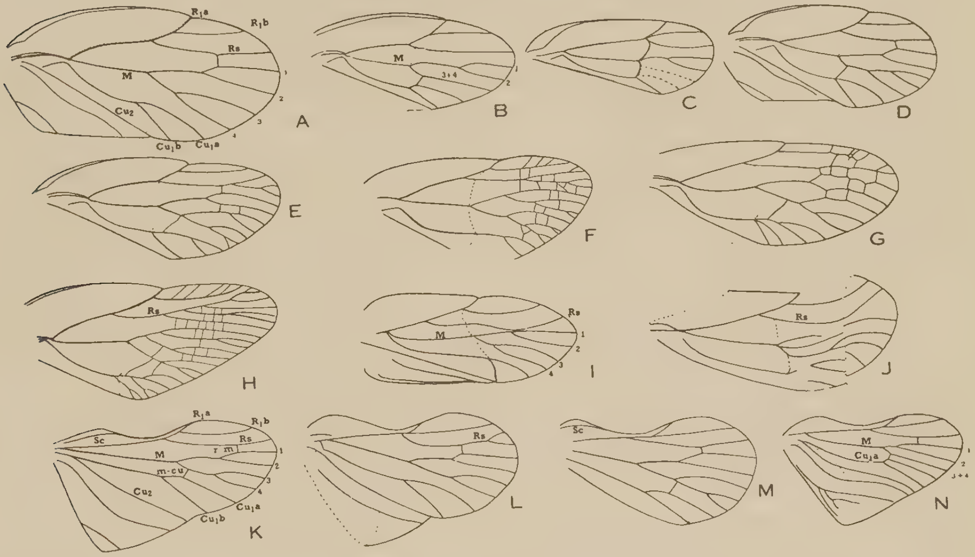

Fig. 10.—*A, Prosbole reducta; B, Permocicada simulatrix; C, Sojanoneura marginata; D, Prosbole reducta; E, P. similis; F, P. hirsuta; G, P. elongata; H, P. triangularis; I, Austroprosbole maculata; J, Permodipthera robusta; K, Prosbole ivagorae; L, P. biexcisa; M, P. brevialata; N, Sojanoneura furculata.*

SOJANONEURA MARGINATA Martynov

Fig. 10*C*

Sojanoneura marginata Martynov, 1930, Trav. Mus. Geol. U.R.S.S. 8: 167 (Permian, Russia).

Martynov stated that this wing was very close to *S. edemskii* but, while the venation is similar, the wing differs in having the nodal division in alignment with the transverse veins. Furthermore, the flexible apex of the wing is shorter. This wing superficially resembles those of many Heteroptera, but in wings of the latter it is usually difficult to determine the identity of the veins distal of the nodal division.

PERMOCICADA UMBRATA Martynov

Permocicada umbrata Martynov, 1928, Trav. Mus. Geol. U.R.S.S. 4: 20 (Permian, Russia).

Permocicada umbrata Martynov, Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 37.

Similar venation to *Prosbole propinqua.*

PROSBOLE SIMILIS Bekker-Migdisova

Fig. 10*E*

Prosbole similis Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 15 (Permian, Russia).

This is the first specialized prosbolid to be considered. The tegmen differs from that of generalized forms not only in venational features, but also in shape and proportions. Accessory veins are present in association with *Rs, M,* and Cu_1 and the flexible apical portion of the tegmen is equal in length and not shorter than the remainder. While this insect and those that immediately follow clearly merit a separate generic designation from those that have already been discussed, for reasons given previously no nomenclatorial change is proposed.

The tegmina of the six species listed below resemble that of *P. similis* in shape and venation:

PROSBOLE DILATATA Martynov

Prosbole dilatata Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 4: 4 (Permian, Russia).

Prosbole dilatata, Martynov, Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 24.

The post-nodal apex of the tegmen is somewhat shorter than that of *P. similis.*

PROSBOLE ZEKKELI Bekker-Migdisova

Prosbole zekkeli Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 16 (Permian, Russia).

PROSBOLE NODOSA Bekker-Migdisova

Prosbole nodosa Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 19 (Permian, Russia).

PROSBOLE INDISTINCTA Bekker-Migdisova

Prosbole indistincta Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 20 (Permian, Russia).

PROSBOLE AFFINIS Bekker-Migdisova

Prosbole affinis Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 19 (Permian, Russia).

PROSBOLE CURVEIMARGINATA Bekker-Migdisova

Prosbole curveimarginata Bekker-Migdisova, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 20 (Permian, Russia).

PROSBOLE SOJANENSIS Martynov

Prosbole sojanensis Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 4: 2 (Permian, Russia).

Prosbole sojanensis Martynov, Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 16.

This tegmen combines the features of those of *P. similis* and *P. elongata* (Figs. 10*E*, 10*G*). The post-nodal apex of the tegmen is not longer than the proximal part and in the illustration given by Martynov additional crossveins, as well as longitudinal ones, are indicated. Bekker-Migdisova has named 3 aberrant tegmina.

PROSBOLE ELONGATA Martynov

Fig. 10*G*

Prosbole elongata Martynov, 1928, Trav. Mus. Geol. U.R.S.S. 4: 16 (Permian, Russia).

Prosbole elongata Martynov, Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 15.

The portion of the tegmen distal of the nodal line is longer than the basal part and more crossveins are present than in *P. similis*.

PROSBOLE CELLULIFERA Bekker-Migdisova

Prosbole cellulifera Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 21 (Permian, Russia).

The tegmen of this species represents a development midway between those illustrated in Figures 10*G* and 10*H*. Increased wing specialization often accompanies increase in size. Thus, while the tegmen of *P. reducta* (Fig. 10*A*) is 17 mm long, that of *P. cellulifera* is 30 mm in length.

PROSBOLE HIRSUTA Handlirsch

Fig. 10*F*

Prosbole hirsuta Handlirsch, 1904, Mém. Acad. Sci. St-Pétersb. 16: 2 (Permian, Russia).

Prosbole hirsuta Handlirsch, 1906, Die Fossilen Insekten, p. 391.

Prosbole ideliana Zalessky, 1930, Bull. Acad. Sci. U.R.S.S., Class Sci. Physico-Math., p. 1018.

Prosbole tchirkoveana Zalessky, 1929, Trav. Soc. Nat. Univ. Kasan 52: 23.

Prosbole hirsuta Handlirsch, Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 22.

This tegmen, which is similar to that of *P. cellulifera,* was the first prosbolid to be described and has been illustrated in many books and papers. In the most recent (Heslop-Harrison 1955*a*) the author, though stating that "ramification is a secondary development" and also that "*Prosbole* is a specialized Homoptera", nevertheless ascribes a "complete medial system" to the tegmen of *P. hirsuta*. By this is meant the full development of both the anterior and posterior branches of *M*, or, in other words, that *M* has 8 branches and that this is a primitive characteristic!

PROSBOLE TRIANGULARIS Martynov

Fig. 10*H*

Prosbole triangularis Martynov, 1935, Bull. Acad. Sci. U.R.S.S., Class. Sci. Math. et Nat., p. 442 (Permian, Russia).

In this tegmen the post-nodal portion of the tegmen is longer than the proximal part and the venation is profusely reticulate.

DICTYOPROSBOLE MEMBRANOSA Martynov

Dictyoprosbole membranosa Martynov, 1935, Bull. Acad. Sci. U.R.S.S., Class. Sci. Math. et Nat., p. 443 (Permian, Russia).

Not only is the venation of this tegmen reticulate beyond the nodal line but there would seem to be a network of fine veins over the whole wing, all of which, and not just the apex, seems to be membranous.

The two species that follow are from the Permian of Australia. Reasons for their inclusion in the Prosbolidae have been given previously:

PERMODIPTHERA ROBUSTA Tillyard

Fig. 10*J*

Permodipthera robusta Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 24 (Upper Permian, New South Wales).

The illustration of this wing has been drawn from the type specimen (in the Collection of the Australian Museum). It differs appreciably from Tillyard's figure. Although the fossil impression is a poor one and is distorted, so far as can be ascertained a nodal line is present. Formerly (Evans 1943) I have associated this genus with others in the family Permoglyphidae.

AUSTROPROSBOLE MACULATA Evans

Fig. 10*I*

Austroprosbole maculata Evans, 1943, Rec. Aust. Mus. 21: 182 (Upper Permian, New South Wales).

This insect was placed in the Prosbolidae at the time of its description and it is proposed to retain it in this family for the time being although it is certainly not closely related to Russian forms. Heslop-Harrison (1951) regards this wing as a "true" protopsyllid.

SCYTINOPTERIDAE AND PROSBOLIDAE

Hindwings

Both the fore- and the hindwings of a few fossil leaf-hoppers are known and names have been given to several which are known only from hindwings. Generally speaking hindwings are less informative as relationship-indicators than forewings. Seven hindwings of Permian Homoptera are illustrated in Figures 3 and 10 and also one of a new species from the Upper Triassic of Queensland.

As has been previously pointed out, the hindwings of Archescytinidae frequently, though not invariably, resemble the forewings in shape and in venation.

What may be regarded as the basic type of scytinopterid-prosbolid hindwing venation is indicated in Figure 10*K*. It will be noted that it is identical with that of the tegminal venation. The wing of *Prosbole ivagorae* has a costal depression and a wide anal area and in this respect is "modern" in appearance. If anomalous wings in which secondary branching has taken place (Figs. 10*L*, 10*M*) are ignored, then the principal evolutionary trends are in the direction of a reduction of veins and of *M* in particular.

While the wings of Permian leaf-hoppers differ from those of recent forms, since the former have a more complete venation and lack a marginal vein, that of the Triassic species described below (Fig. 3*O*) shows a close approach to the venation of recent Homoptera.

Genus MESOJASSULA, gen. nov.

The costal margin of the wing has a marked medial depression. R_1a, R_1b, and *Rs* are present. *M* is unbranched and Cu_1 has 2 equal branches. A marginal vein is present.

Type species *Mesojassula marginata*, sp. nov.

MESOJASSULA MARGINATA, sp. nov.

Fig. 3*O*

Greatest length of wing fragment 10 mm; greatest width 5 mm. Holotype wing C1933, Department of Geology Collection, University of Queensland, Mt. Crosby, Queensland (Upper Triassic).

The wings discussed below are of insects of which the tegmina are unknown, hence they have not previously been listed, or, if the specific names have received earlier mention, then the wings have some feature of particular interest:

PROSBOLE IVAGORAE Bekker-Migdisova

Fig. 10*K*

Prosbole ivagorae Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 28 (Permian, Russia).

The venation of the wing of this species, as already mentioned, is regarded as the basic type both of the Scytinopteridae and the Prosbolidae.

PROSBOLE PERMOCICADOIDES Bekker-Migdisova

Prosbole permocicadoides Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 28 (Permian, Russia).

The venation is almost identical with that of *P. ivagorae.*

PROSBOLE BIEXCISA Martynov

Fig. 10*L*

Prosbole biexcisa Martynov, 1928, Trav. Mus. Geol. U.R.S.S. 4: 17 (Permian, Russia).

Prosbole biexcisa Martynov, Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 26.

This wing is of interest because of the preservation of the overfolded anal portion. The apically forked R_1 is of no special significance.

PROSBOLE LONGIALATA Bekker-Migdisova

Prosbole longialata Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 27 (Permian, Russia).

In this wing, both M_2 and M_4 are apically forked.

PROSBOLE BREVIALATA Bekker-Migdisova

Fig. 10*M*

Prosbole brevialata Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 26 (Permian, Russia).

M_4 is apically forked.

SOJANONEURA PROXIMA Martynov

Sojanoneura proxima Martynov, 1928, Trav. Mus. Geol. U.R.S.S. 4: 26 (Permian, Russia).

M has 2 apical branches.

SOJANONEURA ZEKKELIANA Bekker-Migdisova

Sojanoneura zekkeliana Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 54 (Permian, Russia).

M is reduced to M_{1+2}, M_3, and M_4.

SOJANONEURA FURCULATA Martynov

Fig. 10*N*

Sojanoneura furculata Martynov, 1935, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 4: 12 (Permian, Russia).

Sojanoneura furculata Martynov, Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 52.

M is reduced to M_1, M_2, and M_{3+4}.

PERMOCICADA INCOMPLETA Bekker-Migdisova

Permocicada incompleta Bekker-Migdisova, 1940, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 11: 43 (Permian, Russia).

The venation is similar to that of *S. zekkeliana.*

PERMOCICADA NIGRONERVOSA Martynov

Permocicada nigronervosa Martynov, 1930, Trav. Mus. Geol. U.R.S.S. 8: 166 (Permian, Russia).

An incomplete wing with M as in *S. furculata.*

SCYTINOPTERA REDUCTA (Martynov)

Fig. 3*L*

This species has been discussed previously. M is reduced to 2 branches.

SCYTINOPTERA MACULATA Martynov

Scytinoptera maculata Martynov, 1928, Trav. Mus. Geol. U.R.S.S. 4: 31 (Permian, Russia).

The venation is similar to that of *S. reducta.*

MITCHELLONEURA PERMIANA Tillyard

Mitchelloneura permiana Tillyard, 1922, Proc. Linn. Soc. N.S.W. 46: 415 (Upper Permian, New South Wales).

Mitchelloneura permiana Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 24.

This wing, which Tillyard ascribed to the Prosbolidae, is only partially preserved. M consists of M_1, M_2, and M_{3+4}. Cu_1 is normal, and Rs, which arises from R at one-third of the length of the wing from the base, is forked.

ANOMALOSCYTINA METAPTERYX Davis

Fig. 3*M*

Anomaloscytina metapteryx Davis, 1942, Proc. Linn. Soc. N.S.W. 67: 112 (Upper Permian, New South Wales).

Davis placed this in the Scytinopteridae. M has 2 branches.

ANOMALOSCYTINA INCOMPLETA Evans

Anomaloscytina incompleta Evans, 1943, Rec. Aust. Mus. 21: 189 (Upper Permian, New South Wales).

Another wing with a 2-branched M.

PERMOJASSUS AUSTRALIS

Fig. 3*N*

This wing has been mentioned previously. The figure has been drawn from the type specimen (in the Australian Museum Collection) and not copied from Tillyard's illustration.

MESOCIXIELLA PARVULA Martynov

Mesocixiella parvula Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 7: 94 (Lias, Russia).

This wing resembles that of *Mesojassula marginata* in having a marginal vein. R_1, *Rs*, and Cu_1 are normally developed but *M* is anomalous, being multi-branched.

TRANSITIONAL FORMS

The fore- and hindwings of most scytinopterids, prosbolids, and related Palaeozoic and Mesozoic Homoptera have very different venational characteristics from those of representatives of recent families. A few, however, have been recorded, which either closely resemble those of recent cicadelloids, or else belonged to groups which may be regarded as transitional in character but have left no recent representatives.

The insects in this section are dealt with in three family groupings, of which two are new.

Family **STENOVICIIDAE**, fam. nov.

Permian and Triassic Homoptera having the following characteristics in the venation of the tegmen: *Rs*, if present, sometimes arises from *R* at the point of departure of R_1. *M* has either 3 or 2 branches. In instances where there are 2 branches and the base of their common stem extends from crossvein *r-m*, they consist probably of M_3 and M_4. *M* and Cu_1 may be fused basally. If they are present as separate veins, then the basal bend of Cu_1 meets *M* distally of its junction with *R*. The anal veins may be separate or form a *Y*-vein.

This family is created to comprise the following genera: *Stenovicia* Evans, *Apheloscyta* Tillyard, *Permagra* Evans, *Permovicia* Evans, *Palaeovicia* Evans, *Stenovicia* Evans, *Stanleyana* Evans, and *Permocentrus*, gen. nov. Five of these genera have formerly (Evans 1943) been included in the Ipsviciidae.

The most striking venational feature is the basal fusion of *M* and Cu_1. Two groups of recent Homoptera also have this characteristic, the Cercopoidea and most of the Membracidae. It will be seen from Figure 16*C*, which represents the tegmen of a Triassic cercopid, that the venation of the Stenoviciidae is very different from that of the Cercopoidea. In regard to possible membracid affinities, since some recent membracids have *M* and Cu_1 distinct basally (e.g. *Xiphistes tuberculatus* (Fig. 14*B*)) the fusion of these veins in the tegmina of Membracidae, as shown in Figure 14*D*, may be a comparatively recent development not ante-dating the Tertiary.

Genus PERMOCENTRUS, gen. nov.

There are 2 oblique veins on the forewing between R_1a and R_1b. R_1 is linked with *Rs* by 3 crossveins, and there is a crossvein *r-m*. *M* has

2 branches (?M_3 and M_4). Cu_1 is not arched basally and in Tillyard's figure of the tegmen of the type species it is shown as completely separated from *M*.

Type species *Permoscarta trivenulata* Tillyard.

PERMOCENTRUS TRIVENULATA (Tillyard)

Fig. 11*G*

Permoscarta trivenulata Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 19 (Upper Permian, New South Wales).

Tillyard included this tegmen in the same genus as the Triassic *Permoscarta mitchelli* (Fig. 11*H*), but the presence of *Rs* in *P. trivenulata* and its absence in *P. mitchelli* is sufficient reason for the separation of the two species into different genera.

P. trivenulata differs from some of the other tegmina illustrated in Figure 11 in having *M* and Cu_1 separate basally but resembles *Permagra distincta* (Fig. 11*B*) and *Stenovicia angustata* (Fig. 11*D*) in having *M* apically *Y*-shaped.

STENOVICIA ANGUSTATA Evans

Fig. 11*D*

Stenovicia angustata Evans, 1943, Rec. Aust. Mus. 21: 189 (Upper Permian, New South Wales).

In essential venational features this tegmen closely resembles that of *P. trivenulata*.

PERMAGRA DISTINCTA Evans

Fig. 11*B*

Permagra distincta Evans, 1943, Trans. Roy. Soc. S. Aust. 67: 7 (Upper Permian, New South Wales).

It is not known whether *M* and Cu_1 are joined basally but this tegmen resembles those of *S. angustata* and *Permocentrus trivenulata* in having *M* apically *Y*-shaped. Pronotal paranota are developed.

PERMOVICIA OBSCURA Evans

Fig. 11*C*

Permovicia obscura Evans, 1943, Rec. Aust. Mus. 21: 189 (Upper Permian, New South Wales).

The tegmen of this insect resembles that of *Permagra distincta* in the development of R_1 and *Rs*, and *S. angustata* in the basal fusion of *M* and Cu_1. The apical condition of *M* is unknown.

STANLEYANA PULCHRA

Fig. 11*E*

Stanleyana pulchra Evans, 1943, Rec. Aust. Mus. 21: 188 (Upper Permian, New South Wales).

Rs is lacking, *M* has 3 branches, and *M* and Cu_1 are basally fused.

PALAEOVICIA INCERTA Evans

Fig. 11*F*

Palaeovicia incerta Evans, 1943, Rec. Aust. Mus. 21: 189 (Upper Permian, New South Wales).

The venation of this tegmen may provide a guide to the identity of the branches of *M* in Figures 11*B*, 11*D*, and 11*G*, and seem to suggest that the *Y*-vein shown in these three figures represents M_3 and M_4.

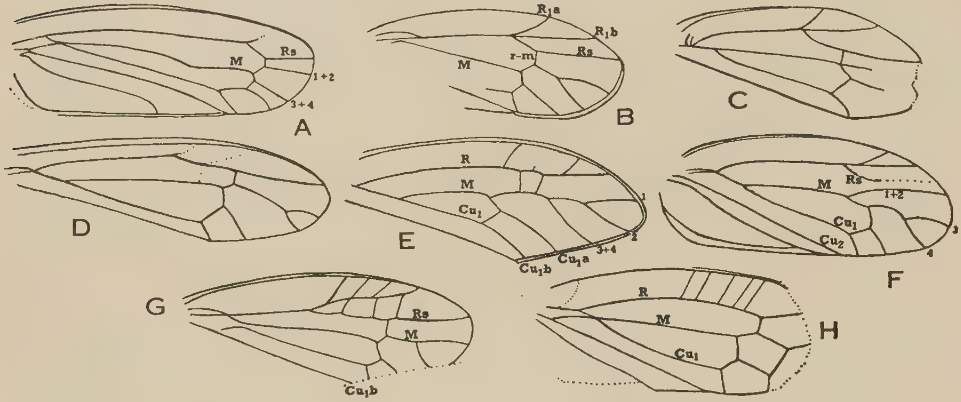

Fig. 11.—*A, Apheloscyta mesocampta; B, Permagra distincta; C, Permovicia obscura; D, Stenovicia angustata; E, Stanleyana pulchra; F, Palaeovicia incerta; G, Permocentrus trivenulata; H, Permoscarta mitchelli.*

APHELOSCYTA MESOCAMPTA Tillyard

Fig. 11*A*

Apheloscyta mesocampta Tillyard, 1922, Proc. Linn. Soc. N.S.W. 47: 459 (Upper Triassic, Queensland).

This tegmen, and the one following, are placed in the family Stenoviciidae for convenience since, while they differ in venation from those of other representatives of the family, they have no special characteristics to merit the creation of another grouping. The interpretation of *M* indicated in the figure may be incorrect.

PERMOSCARTA MITCHELLI Tillyard

Fig. 11*H*

Permoscarta mitchelli Tillyard, 1919, Proc. Linn. Soc. N.S.W. 44: 875 (Upper Triassic, Queensland).

The illustration of this tegmen has been drawn from the type specimen (in the Australian Museum) and not copied from Tillyard's figure from which it differs appreciably. The presence of 2 crossveins between *M* and Cu_1 is an unusual feature.

Family **CHILIOCYCLIDAE**, fam. nov.

Triassic and Jurassic Homoptera having tegmina in which an enclosed cell is formed between the arms of M_{1+2} and M_{3+4}. Cu_1 may have a basal bend or be linked with M by a crossvein, and Rs is invariably present.

CHILIOCYCLA SCOLOPOIDES Tillyard

Fig. 12*F*

Chiliocycla scolopoides Tillyard, 1919, Proc. Linn. Soc. N.S.W. 44: 868 (Upper Triassic, Queensland).

Chiliocycla scolopoides Tillyard, 1922, Proc. Linn. Soc. N.S.W. 47: 460.

The vein labelled Sc in the figure is as shown by Tillyard, but it is of doubtful actual occurrence. This is because the photographic illustration of the fossils suggests that they are not sufficiently well preserved to permit certain identification of the veins at the base of the tegmen. The surface of the tegmen is tuberculate. The possible cercopoid affinities of this insect are discussed under *Procercopina asiatica*.

TIPULOIDEA RHAETICA Wieland

Fig. 12*A*

Tipuloidea rhaetica Wieland, 1925, Amer. J. Sci. 9: 21 (Rhaetic, S. America).

Tipuloidea rhaetica Wieland, Tillyard, 1926, Amer. J. Sci. 11: 265.

This is one of the few tegmina of Mesozoic Homoptera to have been recorded from South America.

TRIASSOJASSUS PROAVITTUS Tillyard

Fig. 12*D*

Triassojassus proavittus Tillyard, 1919, Proc. Linn. Soc. N.S.W. 44: 887 (Upper Triassic, Queensland).

This tegmen, in essential venational features, bears a close resemblance to that of *Archijassus geinitzi* (Fig. 12*G*).

MESOSCYTINA AUSTRALIS Tillyard

Fig. 12*B*

Mesoscytina australis Tillyard, 1919, Proc. Linn. Soc. N.S.W. 44: 870 (Upper Triassic, Queensland).

If the illustration (after Tillyard) is correct then Sc is retained in this wing. It is of interest also as either lacking Rs or else in having it arising from R close to the apex of the wing.

MESOCIXOIDES TERMIONEURA Tillyard

Fig. 12*E*

Mesocixoides termioneura Tillyard, 1922, Proc. Linn. Soc. N.S.W. 47: 462 (Upper Triassic, Queensland).

Ascribed by Tillyard to the Cixiidae. The proximal bend of Cu_1 is more distally placed than in representatives of the Scytinopteridae.

MESOCIXOIDES ORTHOCLADA Tillyard

Mesocixoides orthoclada Tillyard, 1922, Proc. Linn. Soc. N.S.W. 47: 463 (Upper Triassic, Queensland).

The venation of this tegmen is very different from that of the preceding species, but it is impossible to determine its position since the apex is poorly preserved. R_1a arises from R close to the departure of Rs and Cu_1 lacks a proximal bend.

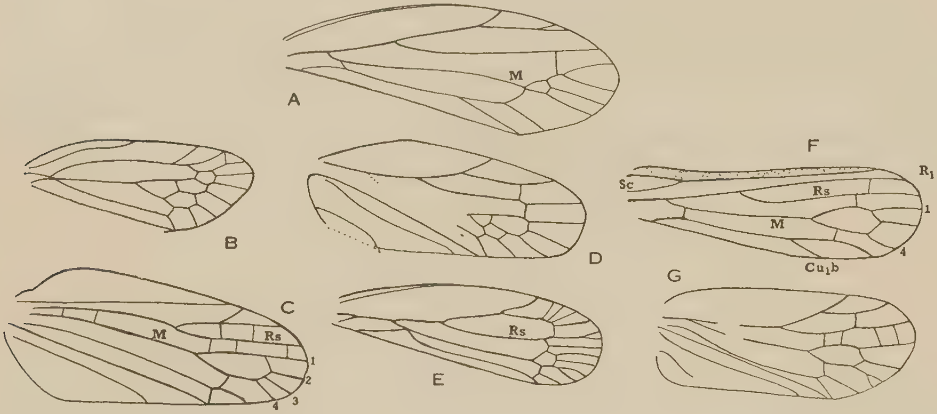

Fig. 12.—*A*, *Tipuloidea rhaetica; B*, *Mesoscytina australis; C*, *Archijassus heeri; D*, *Triassojassus proavittus; E*, *Mesocixoides termioneura; F*, *Chiliocycla scolopoides; G*, *Archijassus geinitzi.*

ARCHIJASSUS HEERI (Geinitz)

Fig. 12*C*

Cercopidium heeri Geinitz, 1880, Z. dtsch. geol. Ges. 1880: 529 (Upper Lias, Germany).

Archijassus heeri (Geinitz), Handlirsch, 1906, Die Fossilen Insekten, p. 501.

Originally described as a cercopid and transferred to the Jassidae by Handlirsch. Since most recent cercopids and no recent cicadellids have Sc lying away from the costal margin of the tegmen, the original placing might appear justified. However, this wing is undoubtedly that of a cicadelloid and the apparent Sc may represent no more than a superficial ridge.

ARCHIJASSUS GEINITZI Handlirsch

Fig. 12*G*

Archijassus geinitzi Handlirsch, 1906, Die Fossilen Insekten, p. 501 (Upper Lias, Germany).

The principal difference between this wing and that of *A. heeri* is the presence of an extensive costal area in the latter.

ARCHIJASSUS VICINUS Handlirsch

Archijassus vicinus Handlirsch, 1939, Ann. naturh. (Mus.) Hofmus., Wien **49**: 144 (Lias, Dobbertin).

This tegmen is of particular interest since, while Cu_1 is proximally bent, *Rs* and *M* closely adjoin each other, foreshadowing the development found in recent cicadellids where these 2 veins are fused together. Handlirsch regarded R_1 as *Sc* and labelled the (?) vein lying between *R* and the costal margin as *C* (see Fig. 12*C*).

LIOJASSUS AFFINIS Handlirsch

Liojassus affinis Handlirsch, 1939, Ann. naturh. (Mus.) Hofmus., Wien **49**: 146 (Lias, Dobbertin).

This tegmen is similar to that of *A. heeri* and differs in that 2 parallel veins are indicated in Handlirsch's figure as lying between *R* and the costal margin.

MESOLEDRA PACHYNEURUS (Handlirsch)

Mesojassus pachyneurus Handlirsch, 1939, Ann. naturh. (Mus.) Hofmus., Wien **49**: 145 (Lias, Dobbertin).

The new name *Mesoledra* is proposed since *Mesojassus* Handlirsch is preoccupied by *Mesojassus* Tillyard (1916). As with other Liassic leafhoppers, a subcostal vein appears to be present between *R* and the costal margin.

Family **EURYMELIDAE** Evans

MESOJASSUS IPSVICIENSIS Tillyard

Fig. 13*A*

Mesojassus ipsviciensis Tillyard, 1916, Qd. Geol. Surv. Publ. **253**: 35 (Upper Triassic, Queensland).

Mesojassus ipsviciensis Tillyard, 1919, Proc. Linn. Soc. N.S.W. **44**: 886.

This tegmen was considered by Tillyard as a cicadellid. I am referring it to the Eurymelidae because of the absence of *Rs* and the retention of M_{1+2} as a separate vein.

Family **CICADELLIDAE** Latreille

EURYMELIDIUM AUSTRALE Tillyard

Fig. 13*C*

Eurymelidium australe Tillyard, 1919, Proc. Linn. Soc. N.S.W. **44**: 885 (Upper Triassic, Queensland).

Tillyard regarded this tegmen as that of a cicadellid and suggested that it resembled those of insects in the recent genus *Eurymela* Le P. & Serv. At that time the family Eurymelidae had not been recognized as a group distinct from the Cicadellidae. Because of the presence of *Rs*, with which M_{1+2} is in part incorporated, this wing would seem to be that of the earliest recorded cicadellid.

Acocephalites breddini Meunier

Acocephalites breddini Meunier, 1904, Feuill. Jeun. Nat. **34**: 119 (Jurassic, Spain).

Acocephalites breddini Meunier, Handlirsch, 1906, Die Fossilen Insekten, p. 643.

This tegmen resembles those of recent cicadellids in all essential features.

Jassites punctatus (Brodie)

Fig. 13*D*

Cicada punctata Brodie, 1845, Fossil Insects, **33**: 120 (Jurassic, England).

Jassites punctatus (Brodie) Handlirsch, 1906, Die Fossilen Insekten, p. 642.

This tegmen, which was regarded by Handlirsch as being of uncertain position, is undoubtedly that of a cicadellid.

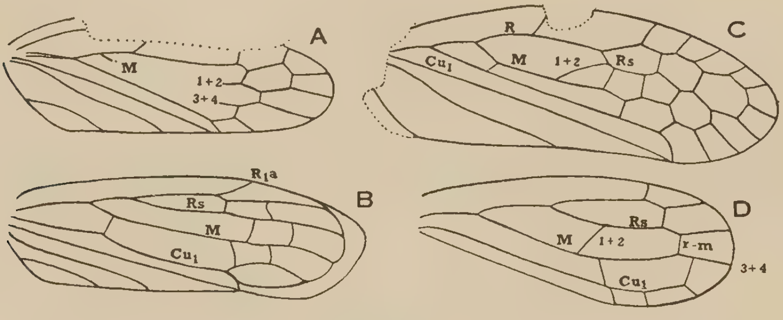

Fig. 13.—*A, Mesojassus ipsviciensis; B, Mesojassoides gigantea; C, Eurymelidium australe; D, Jassites punctatus.*

Cicadellium pulcher (Brodie)

Delphax pulcher Brodie, 1845, Fossil Insects, **33**: 120 (Jurassic, England).

Pseudodelphax pulcher (Brodie), Handlirsch, 1906, Die Fossilen Insekten, p. 641.

Cicadellium pulcher (Brodie), Handlirsch, 1939, Ann. naturh. (Mus.) Hofmus., Wien **49**: 163.

Handlirsch regarded this tegmen as that of a fulgoroid but in my opinion it is more probably that of a cicadellid.

Homopterulum signoreti (Westwood)

Cercopidium signoreti Westwood, 1854, Quart. J. Geol. Soc. **10**: 390 (Jurassic, England).

Homopterulum signoreti (Westwood), Handlirsch, 1906, Die Fossilen Insekten, p. 642.

Homopterulum signoreti (Westwood), Handlirsch, 1939, Ann. naturh. (Mus.) Hofmus., Wien **49**: 163.

Although Handlirsch considered this tegmen as being of uncertain position, it is almost certainly from a cicadellid.

MESOJASSOIDES GIGANTEA Oman

Fig. 13*B*

Mesojassoides gigantea Oman, 1937, J. Paleont. 11: 38 (Cretaceous, N. America).

While the shape of this wing suggests relationship with leaf-hoppers in the recent genus *Tartessus* Stål in venational characters and the wide apical border, it approaches more closely the genus *Coelidea* Germar.

THE VENATION OF RECENT CICADELLOIDEA IN RELATION TO THAT OF FOSSIL FORMS

Forewings

In Figure 14 are illustrated the basic types of tegminal venation of the various families of recent Cicadelloidea, and in Figure 15 the range of venational differences which occur within a single family, the Eurymelidae.

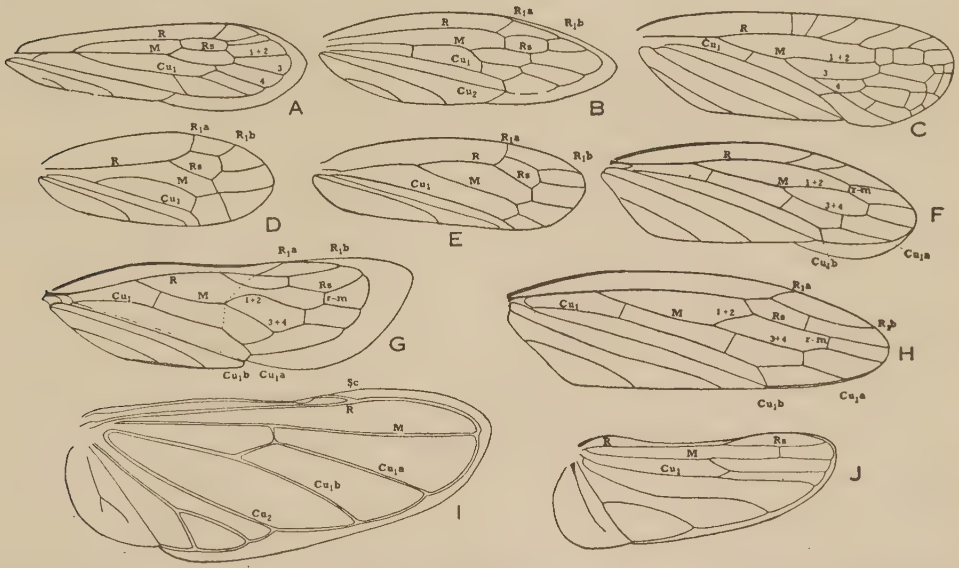

Fig. 14.—*A*, *Nicomia cicadoides*; *B*, *Xiphistes tuberculatus*; *C*, *Aetalion reticulatum*; *D*, *Stegaspis galatea*; *E*, *Mina aliena*; *F*, *Eurymelessa bicincta*; *G*, *Balala fulviventris*; *H*, *Putoniessa nigra*; *I*, *Darthula hardwickii*; *J*, *Coloborrhis corticina*.

If the tegmina of *Nicomia cicadoides* Walker (Fig. 14*A*) and *Aetalion reticulatum* L. (Fig. 14*C*) are excepted, and they are both of relict forms, it will be noted that with all the others, 4 veins extend to the apex of the tegmen. The identity of these veins is different in the various groups. Thus M may have 2 complete branches (Fig. 14*F*), M_{1+2} may be incorporated in the same vein as Rs (Fig. 14*H*), or M_{3+4} may be incorporated in the same vein as Cu_1a (Fig. 14*G*).

Although selection has acted independently to effect vein reduction, a tendency has persisted, at the same time, for vein-proliferation ranging from the addition of a few accessory veins to the development of a reticulate condition. Such a condition is always a secondary one and not, as many have formerly supposed, the retention of an archaic characteristic.

In Figure 15 the progressive reduction of *M* is shown in representatives of a single family from a 4-branched (Fig. 15*A*), to a 2-branched (Fig. 15*D*), by way of a 3-branched condition (Fig. 15*B*). As *Rs* is always absent in the Eurymelidae, *M* is never reduced further than this. Figure 15*E* is an illustration of a tegmen with a highly specialized venational pattern. Reticulate venation occurs also in many tribes and subfamilies of the Cicadellidae, as for example in the Ulopini, Ledrini, Stenocotini, Tettigellinae, Melicharellinae, Gyponini, and Euscelinae.

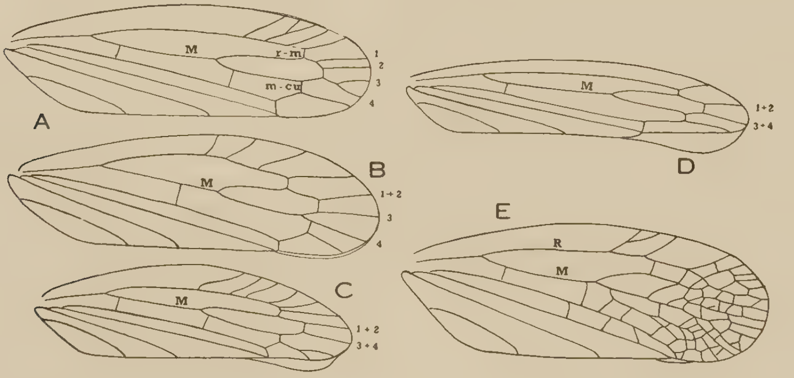

Fig. 15.—*A*, *Eurymelita terminalis; B*, *Australoscopus whitei; C*, *Ipoella fulva; D*, *Bakeriola procurrens; E*, *Eurymela fenestrata.*

Heslop-Harrison (1955*b*) has given figures of his concept of the basic type of jassine and membracine venation. It is difficult, as yet, to offer any reasoned comment on his views since the author, in this paper (Pt. 2 of a series), states that the evidence on which his conclusions are based will be presented in future parts. Nevertheless, as his hypothetical basic plan of homopterous venation appears to be very largely derived from that of a highly specialized prosbolid, it is to be expected that his interpretation of the venation of recent forms will differ widely from my own. Heslop-Harrison's interpretation of *M* has already been queried and all that need be mentioned here is the fact that it would seem that he only recognizes 1 crossvein, *r*, in his "jassine type of venation" and crossveins *r-m* and *m-cu* are regarded by him as branches of *M*. Reference to Figure 2*E* will show that several crossveins additional to *r* were present in Permian tegmina with complete venation. The only additional one acquired by recent cicadellids is the most distally placed *r-m*. This may actually consist of M_4 and the vein labelled Cu_1a in Figure 14*H* may comprise $Cu_1 + M_4$.

Hindwings

While previously (Evans 1946*a*) I have sought to interpret the venation of the forewings of recent Homoptera by establishing homologies with fossil forms, I have refrained from doing so in the case of hindwings and have followed Metcalf's (1913) interpretation. Further study suggests that the venation of the hindwings of recent cicadelloids is as follows:

Aetalionidae (*Fig.* 14I).—*Rs* lacking; *M* single, but possibly in part also incorporated in Cu_1a; 1*A* and 2*A* forming a *Y-vein,* but not supporting the anal fold.

Other Families (*Fig.* 14J).—*Rs* present, M_{1+2} a single vein; M_{3+4} and Cu_1a forming a single vein; 1*A* and 2*A* forming a *Y*-vein and the latter corresponding in position with the anal fold.

Other Structures

In addition to variations in wing venation, Palaeozoic and Mesozoic leaf-hoppers differed from recent forms in the presence, in some species, of pronotal paranota (e.g. *Permocicadopsis angustata, Scytinoptera cubitalis, Triassoscytinopsis paranotalis*) and in others of a median ocellus (*S. cubitalis*). No recent cicadelloids have a median ocellus, but small, though distinct, paranota are retained by species in the genera *Myerslopia* Evans and *Paulianiana* Evans.

Another feature in which early leaf-hoppers may have differed from recent forms is in the possession of better-developed tymbals. This suggestion is put forward since *Darthula hardwickii,* which retains more archaic features than any other still living cicadelloid, has prominent tymbals. Since the time of the development of birds, daylight song of a pitch audible to them will have been of a disadvantage to large insects living and feeding in exposed situations. The reason that cicadas have managed to survive the advent of birds is doubtless because their immature stages are passed underground.

Superfamily **CERCOPOIDEA**

The tegmina of recent cercopoids (Fig. 19) may readily be distinguished from those of recent cicadelloids, but it is not so simple to recognize fossil material. The two new genera and species described below are undoubted representatives of this superfamily, but there is less certainty about the true position of some of the others considered in this section.

Family **CERCOPIDAE** Leach

Genus TRIFIDELLA, gen. nov.

The surface of the tegmen is rugose. There is a series of transverse accessory veins between *R* and the costal margin and others associated with R_1. *Rs* is oblique and *M*, which is proximally incorporated in the same vein as Cu_1, has 2 short branches, each of which is apically forked. Crossveins *r*, *r-m*, and *m-cu* are present.

Type species *Trifidella perfecta*, sp. nov.

TRIFIDELLA PERFECTA, sp. nov.

Fig. 16*C*

Length of tegmen 7 mm; greatest width 4.2 mm. Holotype tegmen C945, Department of Geology Collection, University of Queensland, Mt. Crosby, Queensland (Upper Triassic). Counterpart C946.

This is the earliest recorded wing of a cercopid. It should be compared with the tegmen of the recent *Aufidus tripars* Walker (Fig. 19*C*) which it closely resembles. It is possible that *Sc* is incorporated in the same vein as *R* and that the 2 veins are apically separate in both *T. perfecta* and *A. tripars*.

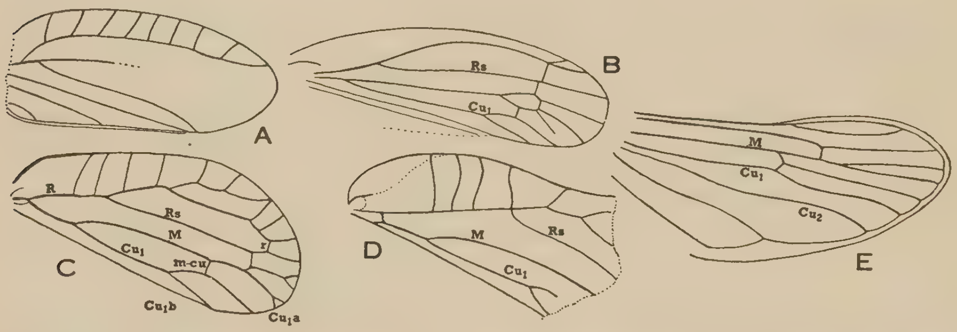

Fig. 16.—*A*, *Triassocarta subcostalis*; *B*, *Procercopina asiatica*; *C*, *Trifidella perfecta*; *D*, *Alotrifidus interruptus*; *E*, *Procercopis jurassica*.

Genus ALOTRIFIDUS, gen. nov.

The costal margin is arched and the costal space wide. *Rs* arises from *R* nearer to the apex of the tegmen than to its base. *M* and Cu_1 form a single vein proximally.

Type species *Alotrifidus interruptus*, sp. nov.

Alotrifidus differs from *Trifidella* in the shape of the costal margin and in the position of the point of departure of *Rs* from *R*.

ALOTRIFIDUS INTERRUPTUS, sp. nov.

Fig. 16*D*

Length of fragment of tegmen 5 mm; greatest width 2.5 mm. The surface is evenly coarsely rugose and the fossil impression is brown in colour with the veins black. Holotype tegmen C347, Department of Geology Collection, University of Queensland, Mt. Crosby, Queensland (Upper Triassic). Counterpart C348.

TRIASSOCARTA SUBCOSTALIS Tillyard

Fig. 16*A*

Triassocarta subcostalis Tillyard, 1919, Proc. Linn. Soc. N.S.W. 44: 874 (Upper Triassic, Queensland).

This tegmen is included in the Cercopidae since such part of the venation as is preserved suggests similarity with the venation of *Trifidella perfecta.* Previously it had been placed in the Scytinopteridae.

The following genera of Liassic Homoptera have been previously placed in the family Procercopidae Handlirsch (1906): *Procercopis* Handlirsch, *Procercopina* Martynov, *Archicercopis* Handlirsch, *Eocercopis* Handlirsch, *Cercoprisca* Handlirsch, *Cercopinus* Handlirsch, *Atitizon* Handlirsch.

Apart from species in the genera *Procercopis* and *Procercopina,* which are discussed below, and *Atitizon jassoides* Handlirsch, which is too poorly preserved to permit classification, species in none of the other genera listed above are recognized as cercopids and all are transferred to a new family, the Actinoscytinidae.

PROCERCOPIS ALUTACEA Handlirsch

Procercopis alutacea Handlirsch, 1906, Die Fossilen Insekten, p. 500 (Upper Lias, Germany).

This is a long (17.5 mm) wing with venation which is basically similar to that of *Procercopina asiatica* (Fig. 16*B*), except for the fact that *M,* which has 2 principal and 1 subsidiary branch, lacks a median cell, and is basally separate from Cu_1.

PROCERCOPIS JURASSICA (Geinitz)

Fig. 16*E*

Cercopis jurassica Geinitz, 1884, Z. dtsch. geol. Ges. 1884: 581 (Upper Lias, Germany).

Procercopis jurassica (Geinitz), Handlirsch, 1906, Die Fossilen Insekten, p. 501.

This is a well-preserved hindwing, which might equally well have belonged to a representative of other groups of Mesozoic Homoptera.

PROCERCOPIS LIASINA Handlirsch

Procercopis liasina Handlirsch, 1906, Die Fossilen Insekten, p. 501 (Upper Lias, Germany).

A fragment of a hindwing.

PROCERCOPIS SIMILIS Handlirsch

Procercopis similis Handlirsch, 1939, Ann. naturh. (Mus.) Hofmus., Wien 49: 142 (Upper Lias, Germany).

A fragment of a hindwing.

PROCERCOPINA ASIATICA Martynov

Fig. 16*B*

Procercopina asiatica Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 7: 10 (Lias, Russia).

This species is represented by a hindwing as well as a forewing. The venation of the latter resembles that of *Procercopis jurassica* in having a 2-branched *M*. As it is also similar in some respects to that of tegmina of certain of the Chiliocyclidae, in particular *Chiliocycla scolopoides* (Fig. 12*F*), it is necessary to explain why 2 wings with a similar venational pattern have been ascribed to different superfamilies.

The cercopoid features of the tegmen of *P. asiatica* are the apparent presence of a short *Sc* apically directed towards the base of *R* and the basal fusion of *M* and Cu_1. The principal cicadelloid features are the branched condition of *M* and the development of a medial cell.

The tegmen of *C. scolopoides* also has an apparent short *Sc*, but it terminates at the costal border and the only other possibly cercopoid feature is the tuberculate surface which resembles that of *Trifidella perfecta*. It is suggested, that if a mistake has been made in the placing of either the tegmen of *P. asiatica* or of *C. scolopoides*, then the error most probably lies in ascribing the former to the Cercopoidea rather than the latter to the Chiliocyclidae.

Family **DYSMORPHOPTILIDAE** Handlirsch

In 1906, Handlirsch created this family for the reception of a wing from the Lower Lias of England. Certain wings found in Upper Triassic strata in Queensland bear a striking resemblance to this Liassic wing and are accordingly included in the same family.

DYSMORPHOPTILA LIASINA (Giebel)

Fig. 17*C*

Belostoma liasina Giebel, 1856, Ins. Vorw. p. 371 (Lower Lias, England).

Dysmorphoptila liasina (Giebel), Handlirsch, 1906, Die Fossilen Insekten, p. 492.

This wing is 10.5 mm in length. Handlirsch, who pointed out that it had no relationship with *Belostoma*, suggested it might be related to *Scytinoptera*.

Genus DYSMORPHOPTILOIDES, gen. nov.

The forewing is evenly punctate and has a narrow margin. The costal border is emarginate in the neighbourhood of the apex of R_1 and the apex of the wing is narrowly rounded. *R* is approximately parallel with the costal margin with which it is joined by a series of widely-spaced parallel veins. R_1 has 3 branches and the proximal one is in alignment with *R*. *Rs* may be a separate from R_1 for its whole length or be incorporated, in part, in the same vein as R_1. M, which has 4 apical branches of approximately equal length, is joined basally to Cu_1. Cu_1a is greater in length than Cu_1b. Crossveins r, r-m, and m-cu may be present. The clavus is unknown.

Type species *Dysmorphoptiloides elongata*, sp. nov.

Dysmorphoptiloides differs from *Dysmorphoptila* Handlirsch in having a series of oblique costal veins and in a more complete M. The forewings of species in both genera are similar in shape and both have R_1b apically forked.

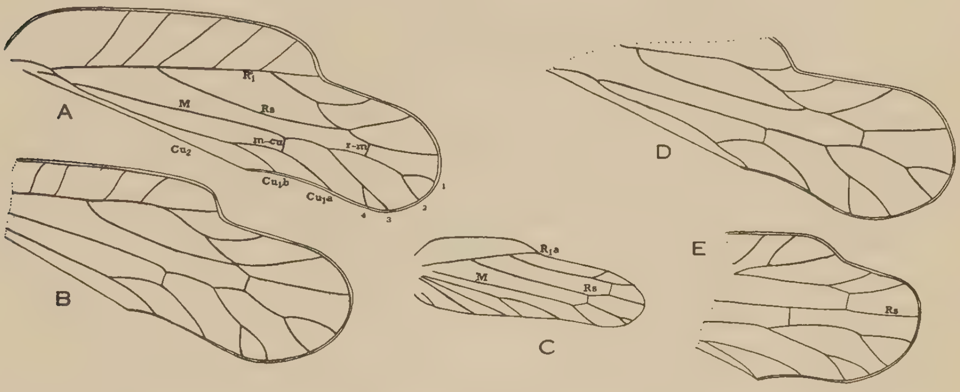

Fig. 17.—*A, Dysmorphoptiloides elongata; B, D. elongata; C, Dysmorphoptila liasina; D, Dysmorphoptiloides elongata; E, D. parva.*

DYSMORPHOPTILOIDES ELONGATA, sp. nov.

Figs. 17*A*, 17*B*, 17*D*

Length of holotype tegmen 16 mm; greatest width 5 mm; width at apex 3.8 mm. Rs meets R_1 ante-apically, and the 2 veins may be fused as one for a short distance. Holotype tegmen C686 (Fig. 17*A*), Department of Geology Collection, University of Queensland, Mt. Crosby, Queensland (Upper Triassic). Other specimens: C950 (counterpart 951), length 12.5 mm (Fig. 17*B*); C614 (counterpart C613), length 15.2 mm (Fig. 17*D*). Unfigured specimens: C1434 (length 16 mm) and C962, C963, a fragment only. In addition there are several specimens in the collection lacking registered numbers.

DYSMORPHOPTILOIDES PARVA, sp. nov.

Fig. 17*E*

Length of whole tegmen 12 mm; greatest width 5 mm. This wing differs from that of the type species in having Rs separate from R_1 for its whole length, a crossvein r, and a less elongated apex. Holotype tegmen C795, Department of Geology Collection, University of Queensland, Mt. Crosby, Queensland (Upper Triassic). Counterpart C794, a complete tegmen but the apex is not so well preserved as in the holotype specimen.

The Dysmorphoptilidae are ascribed to the Cercopoidea for the following reasons: the tegmina of *Dysmorphoptiloides* spp. resemble that of *Trifidella perfecta* (Fig. 16*C*) in all essential venational characteristics, both of a generalized and specialized nature; furthermore, the surface of the tegmina of species in both genera are coarsely rugose.

Family **EOSCARTERELLIDAE**, fam. nov.

Accompanying a letter to *Nature* written by Tillyard and published in 1936 was a photograph of a homopterous wing with the following caption: "Complete tegmen of a specialized scytinopterid type in process of becoming a true heteropterous type." In the letter Tillyard wrote: "This is the first clear indication from palaeontology of the probable mode of origin of the Heteroptera from the older Homoptera." If wing shape and structure were the only features in which representatives of the two suborders differed from each other, then such a statement might be permissible. As, however, the differences are more fundamental, it is of a misleading nature. The wing illustrated by Tillyard is reproduced in Figure 18*B*. In the absence of knowledge of the whereabouts of the fossil specimen it must remain unnamed.

Among the material from Mt. Crosby are tegmina of 2 related insects and these are described below.

Genus EOSCARTERELLA, gen. nov.

Triassic Homoptera with rugose tegmina which increase in width distally. R_1 has more than 2 branches and Rs arises from R at about one-third the length of the tegmen from the base. R and M proximally straight and parallel with each other and basally fused. M with 4 branches. Cu_1 is not fused basally with M and is proximally straight. Cu_1a is arched and considerably larger than Cu_1b.

Type species *Eoscarterella media*, sp. nov.

EOSCARTERELLA MEDIA, sp. nov.

Fig. 18*C*

Length of tegmen 10.5 mm; greatest width 5 mm. Holotype tegmen C1110, Department of Geology Collection, University of Queensland, Mt. Crosby, Queensland (Upper Triassic). The counterpart (C1111) has the apex of the tegmen completely preserved.

Genus EOSCARTOIDES, gen. nov.

The tegmen has a complete marginal border. R and M are basally arched. R_1a and R_1b are both forked. M_1 and M_2 are present as separate veins and M_{3+4} form a single vein. Cu_1 is slightly arched basally and does not meet Cu_2. The 2 branches of Cu_1 are of approximately equal length.

Type species *Eoscartoides bryani*, sp. nov.

EOSCARTOIDES BRYANI, sp. nov.

Fig. 18*A*

Length of tegmen 12 mm; greatest width 6 mm. Holotype tegmen C172, Department of Geology Collection, University of Queensland, Mt. Crosby, Queensland (Upper Triassic). Other specimens: C934 (11 mm)—this has crossvein *m-cu* present; C677 (counterpart C680) (11 mm)—this has crossveins *r*, *r-m*, and *m-cu* present and 2 oblique veins between *R* and the costal border, proximally of R_1a.

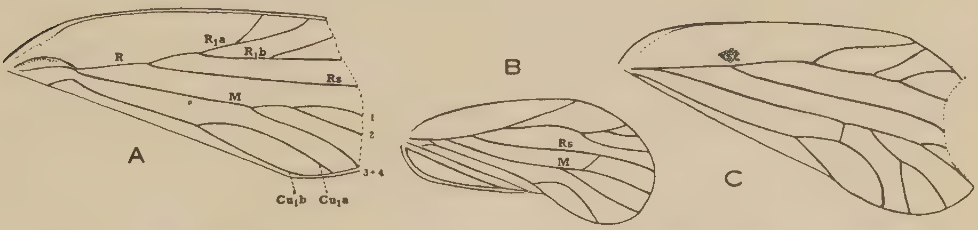

Fig. 18.—*A*, *Eoscartoides bryani; B*, Unnamed wing (Tillyard 1936); *C*, *Eoscarterella media.*

Eoscartoides differs from *Eoscarterella* in the shape of the tegmen and in the shape of the arms of Cu_1.

The Eoscarterellidae are provisionally placed in the Cercopoidea because of the proximal point of derivation of *Rs* from *R*, the presence of accessory veins associated with R_1, the shape of Cu_1, and the rugose structure of the tegmen of *E. media.* They differ from other cercopoids in having Cu_1 separated basally from *M*.

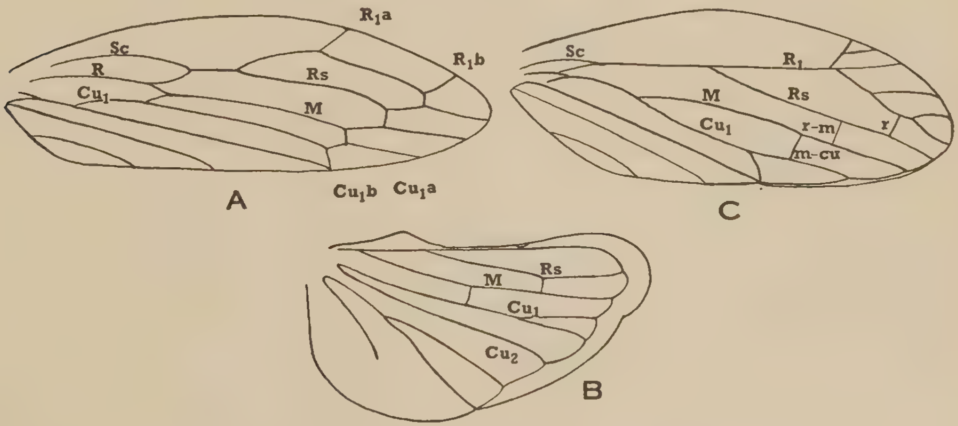

Fig. 19.—*A*, *Philagra parva; B, P. parva; C, Aufidus tripars.*

Superfamily CICADOIDEA

Recent cicadas differ from other Homoptera in several respects and their most divergent characteristic is the anomalous behaviour of their larvae which enter soil soon after hatching and have forelegs adapted for burrowing purposes. Then cicadas alone among the Cicadomorpha (Evans 1946*a*, 1951) have retained a median ocellus. If Bekker-Migdisova is correct in recognizing such an ocellus in the impression of the head of *Scytinoptera cubitalis* (Bekker-Migdisova 1946, Fig. 15) then this characteristic was shared with the immediate ancestors of the Cicadelloidea in late Palaeozoic times. Thanks to the work of Ossiannilsson (1949), it is now known that tymbal sound production in Homoptera is not confined to cicadas. Furthermore, although in most cicadas only the males are vocal, it is probable that both sexes of the relict genus *Tettigarcta* can produce sound, as is the case with other Homoptera. This assumption is contrary to my earlier one (Evans 1941) when at the time I demonstrated the presence of tymbal muscles in species in this genus, I suggested that the tymbals were functionless.

Most cicadas are larger than other recent Homoptera, with the exception of fulgoroids, but there are some which are only 10 mm in length, and this is less than that of several cicadelloids and cercopoids.

Family **CICADOPROSBOLIDAE**, fam. nov.

This family is created to contain the genus *Cicadoprosbole* Bekker-Migdisova, which Bekker-Migdisova (1947) regarded as a transitional form between the Prosbolidae and the Cicadidae but which she placed in the Prosbolidae.

CICADOPROSBOLE SOGUTENSIS Bekker-Migdisova

Fig. 20

Cicadoprosbole sogutensis Bekker-Migdisova, 1947, C.R. Acad. Sci. U.R.S.S. 55:
No! 445 ~~(Permian, Russia)~~. Lower Lias

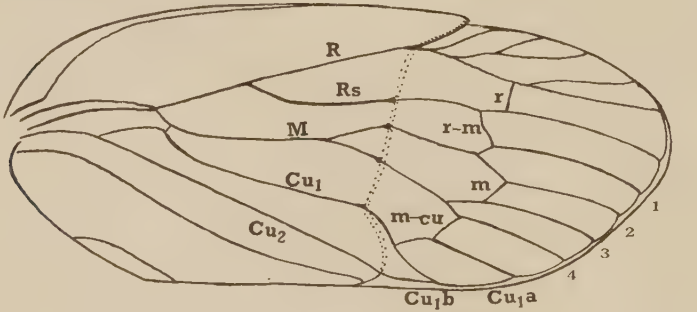

Fig. 20.—*Cicadoprosbole sogutensis.*

Bekker-Migdisova regarded the tegmen of this insect as intermediate in character between *Permocicada integra* (Fig. 2*C*) and *Tettigarcta crinita* Distant (Fig. 24*A*). *P. integra* lacks any indication of the presence of a nodal line and I have considered it as a scytinopterid with complete basic venation. It is more appropriate to compare the tegmen of *C. sogutensis* with that of *Prosbole reducta* (Fig. 10*A*). These 2 tegmina resemble each other in basic venational features but differ in three respects. The tegmen of *C. sogutensis* has some short supplementary veins developed between R_1a and R_1b and has 3 more crossveins than are present in the tegmen of *P. reducta.* One of these crossveins (*m-cu*) is present in the tegmina of related prosbolids with simple, as apart from reticulate, venation, but *r* and *m* are absent in these forms. The third point of difference relates to the position of the nodal line. In *P. reducta* and in other prosbolids this extends from *Rs* close to its point of separation from *R* and intersects *M* where it divides into M_{1+2} and M_{3+4}. In *C. sogutensis* the nodal line crosses *Rs* at a point widely distant from its divergence from R_1 and crosses *M* after it has divided into its 2 primary branches.

If Figure 20 is compared with Figure 24*A* (*T. crinita*) it will be noted that in two out of the three points of difference with *P. reducta* it resembles the tegmen of *T. crinita.* It differs from the latter in having a wider costal space and in the presence of accessory veins between R_1a and R_1b. These differences are, however, of minor significance and it is accordingly suggested that *C. sogutensis* is a true cicada and not a prosbolid with certain cicada-like characteristics.

As it is considered that *Palaeontina oolitica* Butler is not a homopteron, a new family name is necessary to comprise those genera which were formerly included in the Palaeontinidae and which are undoubtedly Homoptera.

When the family Palaeontinidae Handlirsch was created in 1906 it was ascribed to the Lepidoptera, even though some of the included genera had previously been described as Homoptera. Handlirsch regarded the family as one closely related to the Limacodidae.

At one time Tillyard (1918*a*) accepted Handlirsch's opinion but later (Tillyard 1921) he changed his views and suggested that the Palaeontinidae were Homoptera closely related to the Mesogereonidae and with a less close affinity to recent Cicadidae. One of the reasons given by Handlirsch for regarding these insects as Lepidoptera was that scales were visible on the wings of several specimens. Tillyard failed to see such scales and certainly none are apparent on Australian fossil representatives. It is of interest to note, however, that the recent Hylicidae (Evans 1946*b*), another family with prosboloid affinities, have scales and hairs on their forewings.

Family **CICADOMORPHIDAE**, fam. nov.

Large Mesozoic Homoptera having forewings 40 mm or more, in length. As well as having complete venation, *Sc* is usually developed as a separate vein near to the base of the wing. Resembling the Prosbolidae but differing from the Cicadoprosbolidae in the position of the nodal line in relation to M_1 and differing from the Prosbolidae in regard to the position of the nodal line in relation to *Rs*. The most readily recognizable venational characteristic is associated with crossvein *m-cu*. This is either sinuate (Fig. 21*F*), or if straight, then in alignment with M_4. The hindwings resemble the forewings in having complete venation, but differ in shape, particularly in regard to the costal margin. It is possible that both fore- and hindwings had a marginal vein.

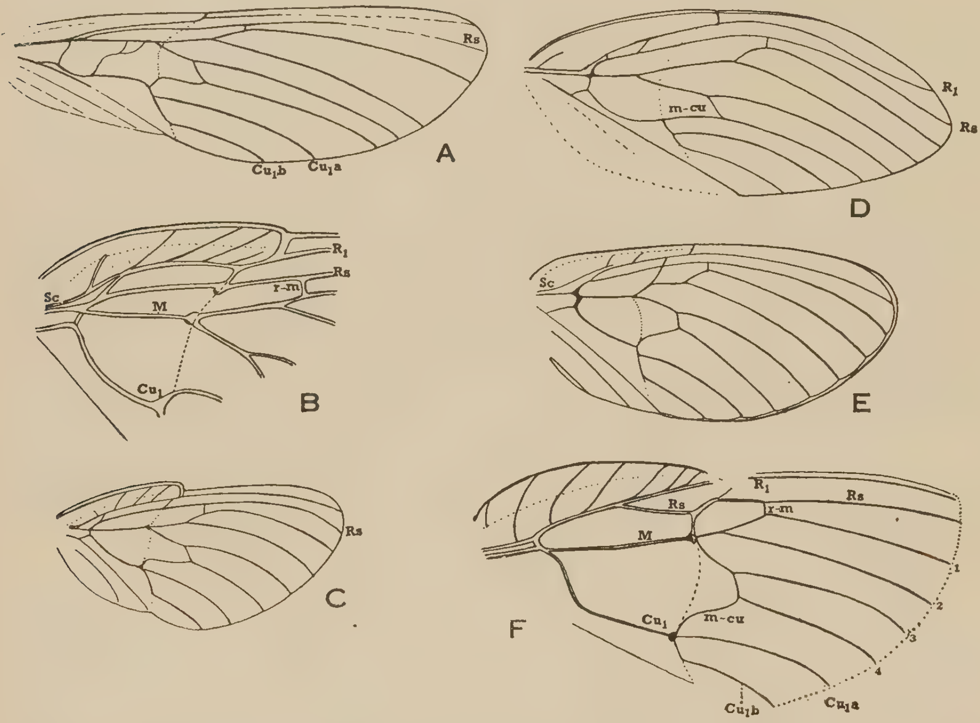

Fig. 21.—*A*, *Palaeontinodes shabarovi; B, Pseudocossus zemcuznikovi; C, P. zemcuznikovi; D, Phragmatoecites damesi; E, Palaeocossus jurassicus; F, Fletcheriana triassica.*

Genus FLETCHERIANA, gen. nov.

Forewing with the costal space wider proximally than distally and with several oblique veinlets. The nodal line, which crosses *Rs* after its point of departure from *R*, is thickened between *Rs* and *M*. *M* with 4 branches. The nodal line crosses *M* at its point of initial separation into M_{1+2} and M_{3+4}. There is a crossvein between *Rs* and M_1; Cu_1 is sharply flexed basally and *M* and Cu_1 are connected by a sinuate crossvein.

The costal margin of the hindwing curves medially towards the retinaculum and there is a narrow border marked with raised dots. *Sc* lies alongside *R* as far as the marginal bay. There is a crossvein between

Rs and M_1. *M* with 4 branches and the 2 first separate from each other at, or near, the point at which the stalk of M_{3+4} departs from *M*. Crossvein *m-cu* straight and not curved as in the forewing.

Type species *Fletcheriana triassica,* sp. nov.

Fletcheriana resembles *Pseudocossus* Martynov in several respects but differs in the shape of the costal area proximally and in having *Rs* arising from *R* in a more distal position.

FLETCHERIANA TRIASSICA, sp. nov.

Figs. 21*F*, 22

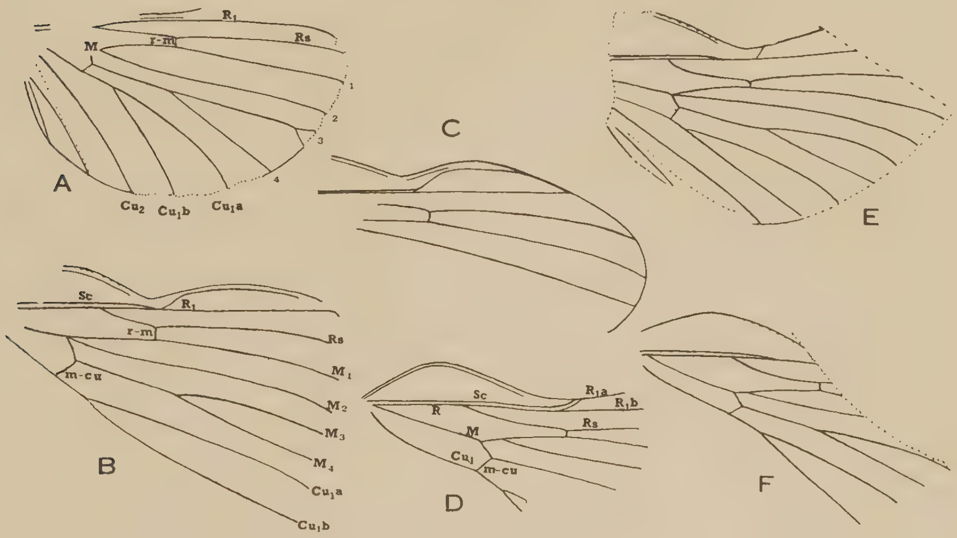

Fig. 22.—*A-F*, Fragments of hind wings of *Fletcheriana triassica.*

Length of holotype forewing 58 mm; greatest width 23 mm. The whole surface of the forewing is pitted and there are oval-shaped pale markings. Holotype forewing F39166 (counterpart F39165).

Length of holotype hindwing 40 mm; greatest width 25 mm. Holotype hindwing F30971 (Fig. 22*A*).

Both wings in the collection of the Australian Museum, from Brookvale Quarry, near Sydney, N.S.W. (Middle Triassic).

Additional Material.—F30952, a whole insect. The length, from the front of the head to the apex of the folded tegmina, is 81 mm and the greatest width of the specimen 45 mm. The venation is obscured by overlapping wings.

Forewings.—F30952 (length 45 mm; greatest width 25 mm). A black impression with large pale oval markings arranged in rows between the veins. The apex of R_1 curves towards the costal margin which it meets close to the apex of the wing. Fragments: F39161; F39162; F39164.

Hindwings.—F39159 (Fig. 22*B*); F26751 (Fig. 22*C*), length 35 mm; F35881 (Fig. 22*D*), a black impression on brown rock, length 30 mm, width 12 mm; F36273 (Fig. 22*E*), a good impression, length 36 mm, width 30 mm; F31960 (Fig. 24*F*), length 35 mm, width 13 mm. Also: F30945, F38261, F39170, F39169, F30968, F39168, F39163, F35880, F30976, F39171. All the above are from Brookvale.

In addition to the wings listed above from the Middle Triassic of New South Wales, a fragment corresponding with part of the hindwing illustrated in Figure 22*E* occurs in the material from Mt. Crosby (C2240, counterpart C2239). The length of the fragment is 22 mm.

PHRAGMATOECITES DAMESI Oppenheim

Fig. 21*D*

Phragmatoecites damesi Oppenheim, 1886, Berl. ent. Z. **29**: 333 (Jurassic, E. Siberia).

Phragmatoecites damesi Oppenheim, Handlirsch, 1906, Die Fossilen Insekten, p. 621.

Phragmatoecites damesi Oppenheim, Martynov, 1931, Ann. Soc. Paleont. Russ. 9: 101.

The illustration reproduced in Figure 21*D*, is taken from Martynov's paper and two features are shown which are almost certainly incorrect and misleading. These are the apparent basal separation of *Rs* from R_1 and the position of the nodal line in relation to *M*. In Handlirsch's illustration of the fossil, but not in his reconstruction, *Rs* would seem to arise from *R* in the same position as is shown in Figure 21*E* and the nodal line to cut *M* transversely just before its first division. Handlirsch (1939) suggested that this wing and the one that follows might be hindwings, but if a comparison is made with *F. triassica,* of which both fore- and hindwings are preserved, then it is evident that both impressions are of forewings.

PALAEOCOSSUS JURASSICUS Oppenheim

Fig. 21*E*

Palaeocossus jurassicus Oppenheim, 1885, Berl. ent. Z. **29**: 333 (Triassic, E. Siberia).

Palaeocossus jurassicus Oppenheim, Handlirsch, 1906, Die Fossilen Insekten, p. 622.

Palaeocossus jurassicus Oppenheim, Martynov, 1931, Ann. Soc. Paleont. Russ. 9: 97.

This forewing is of interest as it resembles those of recent cicadas in the development of a marginal vein.

CICADOMORPHA PUNCTULATA Martynov

Cicadomorpha punctulata Martynov, 1926, Bull. Acad. Sci. U.R.S.S. **20**: 357 (Jurassic, Turkestan).

Although in Martynov's illustration of this forewing no indication is given of the presence of a nodal line, and neither is the characteristic crossvein *m-cu* shown, this tegmen, as was suggested by Martynov, is undoubtedly that of a cicadomorphid.

PSEUDOCOSSUS ZEMCUZNIKOVI Martynov

Figs. 21*B*, 21*C*

Pseudocossus zemcuznikovi Martynov, 1931, Ann. Soc. Paleont. Russ. 9: 94 (Jurassic, E. Siberia).

Attention is drawn to the reduced clavus in relation to the expansion of the rest of the wing.

PALAEONTINODES SHABAROVI Martynov

Fig. 21*A*

Palaeontinodes shabarovi Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 7: 102 (Lower Liassic, Shurab).

The proportions of this forewing are different from those of the others illustrated in Figure 21 but the venation is very similar. The most notable difference is the wide space between Cu_1 and M basally, the lack of a basal bend in Cu_1 and the presence of supporting crossveins.

PALAEONTINOPSIS LATIPENNIS Martynov

Palaeontinopsis latipennis Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 7: 104 (Lias, Shurab).

An undoubted forewing of a cicadomorphid lacking any unusual features.

PALAEONTINOPSIS MAXIMUS Martynov

Palaeontinopsis maximus Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 7: 105 (Lias, Shurab).

A fragment only.

PALAEONTINOPSIS ARCUATUS Martynov

Palaeontinopsis arcuatus Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 7: 105 (Lias, Shurab).

A fragment of a forewing of which the base is not preserved.

The following representatives of the family Palaeontinidae have at some time been regarded as belonging to the order Homoptera: *Palaeontina oolitica*, *Prolystra lithographica* Oppenheim, *Cicadites gigantea* Haase, *Eocicada microcephala* Oppenheim, *Eocicada lameeri* Handlirsch, *Beloptesis oppenheimi* Handlirsch. None of these is recognized here as having homopterous affinities.

Family **MESOGEREONIDAE** Tillyard

The first fragment of a wing to be ascribed to this family was described by Tillyard in 1916 from the Upper Triassic of Queensland and named *Mesogereon neuropunctatum.* Its greatest length was 23 mm and its breadth 17 mm. The fragment is illustrated in Figure 23*D* (after Tillyard 1916). Because of the resemblance of the venational plan to that of *Eugereon,* Tillyard placed the genus in the order Protohemiptera. Later (1921) he described 2 more wings (*M. superbum* and *M. shepherdi*) and 3 fragments (*M. compressum* and *M. affine*), and created the family Mesogereonidae which he ascribed to the Homoptera. The wings and the fragments are illustrated in Figure 23 and, with the exception of Figure 23*A,* have all been copied from Tillyard's figures. The illustration of the wing of *M. superbum* is based on a good photograph of the fossil impression and differs in several respects from Tillyard's figure.

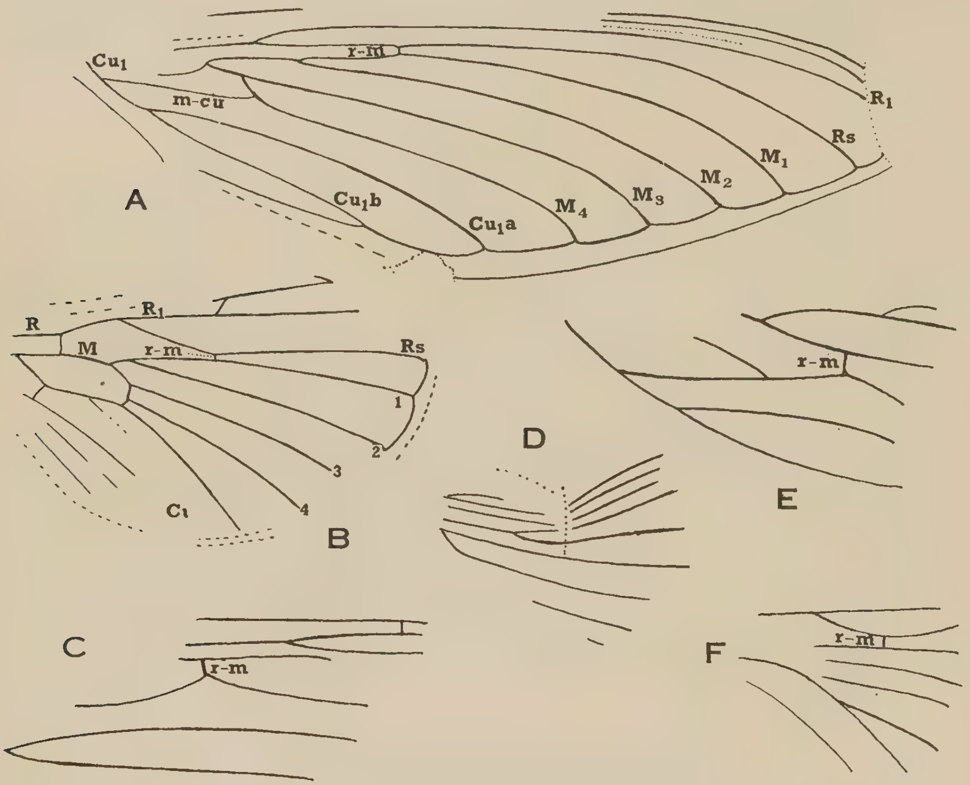

Fig. 23.—*A, Mesogereon superbum; B, M. shepherdi; C, M. compressum; D, M. neuropunctatum; E, M. affine; F, M. affine.*

In his definition of the family Tillyard stated that it comprised large cicada-like insects without sound-producing apparatus and that it was closely related to the Jurassic Palaeontinidae and more remotely to existing Cicadidae.

The various fragments (*M. compressum, M. neuropunctatum,* and *M. affine*) can be disregarded. It remains to discuss whether the wing of *M. superbum* is that of an insect belonging to the Cicadoidea, and also whether *M. shepherdi* is the hindwing of *Mesogereon* sp. or of a cicadomorphid.

It cannot, of course, be determined by wing examination whether or not these insects had sound-producing structures. If the balance of the evidence should suggest that the family is a homopterous one, then it can be supposed that its representatives were vocal.

There is no trace of a nodal line in the wing of *M. superbum.* The proximal separation of *Rs* from *R,* the presence of crossvein *r-m,* and the 4-branched media are all features shared with the Cicadomorphidae, as are likewise the elongated crossvein *m-cu* and the ambient vein.

Tillyard's placing of *M. superbum* in the Cicadoidea is supported. This is contrary to Handlirsch's (1939) opinion that it should be regarded as a homopteron of uncertain position. If Figure 23*A* is compared with Figure 21*A* (*Palaeontinodes shabarovi*) it will be seen that the wing of *M. superbum* may represent a specialized development from a form of cicadomorphid wing. Furthermore, a transverse line of weakness is not to be expected in a wing which has a very small area situated proximally of the position of where a nodal line would lie if present, as in such a position it would be a hindrance and not an asset for flight purposes.

The wing of *M. superbum* is 44.5 mm long and its greatest breadth is 12 mm. The wing of *M. shepherdi* is only 21 mm long. Tillyard did not suggest that the 2 wings belonged to a single species, and hindwings of many recent cicadas are considerably smaller than the forewings. As the wing of *M. shepherdi* differs from the hindwing of *F. triassica* (Fig. 22) in having a crossvein linking *R* with *M* proximally of the departure of *Rs* from *R,* in having a crossvein linking Cu_1 with Cu_2, and in having M_3 and M_4 as separate veins for the whole of the distance beyond crossvein *m-cu,* it is accepted that it may be the hindwing of a *Mesogereon* sp. and not that of a cicadomorphid.

MESOGEREON NEUROPUNCTATUM Tillyard

Fig. 23*D*

Mesogereon neuropunctatum Tillyard, 1916, Qd. Geol. Surv. Publ. **253**: 34, 273 (Upper Triassic, Queensland).

MESOGEREON SUPERBUM Tillyard

Fig. 23*A*

Mesogereon superbum Tillyard, 1921, Proc. Linn. Soc. N.S.W. **46**: 274 (Upper Triassic, Queensland).

MESOGEREON COMPRESSUM Tillyard

Fig. 23*C*

Mesogereon compressum Tillyard, 1921, Proc. Linn. Soc. N.S.W. **46**: 277 (Upper Triassic, Queensland).

MESOGEREON AFFINE Tillyard

Figs. 23*E*, 23*F*

Mesogereon affine Tillyard, 1921, Proc. Linn. Soc. N.S.W. **46**: 277 (Upper Triassic, Queensland).

MESOGEREON SHEPHERDI Tillyard

Fig. 23*B*

Mesogereon shepherdi Tillyard, Proc. Linn. Soc. N.S.W. **46**: 277 (Upper Triassic, Queensland).

HYLAEONEURA LIGNEI Lameere & Severin

Hylaeoneura lignei Lameere & Severin, 1897, Ann. Soc. Ent. Belg. **41**: 35 (Lower Cretaceous, Belgium).

Hylaeoneura lignei Lameere & Severin, Handlirsch, 1906, Die Fossilen Insekten, p. 668.

Hylaeoneura lignei Lameere & Severin, Cooper, 1941, Amer. J. Sci. **239**: 293.

The wing of this insect, of which only a fragment is preserved, was described originally as a sialid but Handlirsch later transferred it to the Cicadidae. Cooper, in a review of fossil cicadas of Tertiary age, correctly rejected it from this family.

DISCUSSION OF THE CICADOIDEA

Myers (1929) discussed the problem of the ancestry of cicadas but made no original contribution.

The wings of some recent representatives are illustrated in Figure 24. The venation of the forewing of *Tettigarcta crinita,* which is not typical of recent cicadas, will first be considered. This has been referred to earlier and attention has been drawn to the close resemblance which exists between it and the venation of the Permian *Cicadoprosbole sogutensis.* Bekker-Migdisova (1940) has suggested that cicadas are almost certainly derived from prosbolids and this is doubtless a correct deduction, but it would seem that *Tettigarcta* lies on a different line of descent from that of all other recent cicadas. Figure 24*D* represents the wing of *Froggattoides typicus* Distant. This wing differs from those of most recent cicadas in shape, the angulate costal margin, and the wide costal cell, but it has essentially the same venational pattern. The venation differs from that of *T. crinita* in the incorporation of *Sc* and *R* in the costal margin, in the fact that *Rs* departs from *R* where it is crossed by the nodal line, and in the reduction of the clavus.

Unlike *T. crinita*, the forewing of *F. typica* resembles that of *Prosbole reducta* (Fig. 10*A*) in the position of the nodal line in relation to *R* and *Rs*. It shares with *T. crinita* the character of the nodal line crossing *M* after its point of initial separation into 2 branches. Both in the Prosbolidae and in the Cicadomorphidae the nodal line crosses *M* before its first division.

The venation of the hindwing of *T. crinita* (Fig. 24*B*) is very similar to that of the hindwings of prosbolids. It differs in the early departure of *Rs* from R_1, in the position of *r-m*, and in the acquisition of crossvein *r*, also in the reduction of *M* from a basic 4- to a 3-branched condition.

The hindwing of *Cystosoma saundersi* Westward (Fig. 24*C*) is similar in venational characteristics to those of most cicadas but differs in having *Rs* branched and the anal area marginally strengthened. The hindwings of cicadas in general resemble those of prosbolids both in shape and in venation more than they do those of cicadomorphids. From a consideration of the available evidence it would seem that while recent cicadas are certainly descended from prosboloid ancestors they cannot have been directly derived from representatives of either known Prosbolidae or from the Cicadomorphidae.

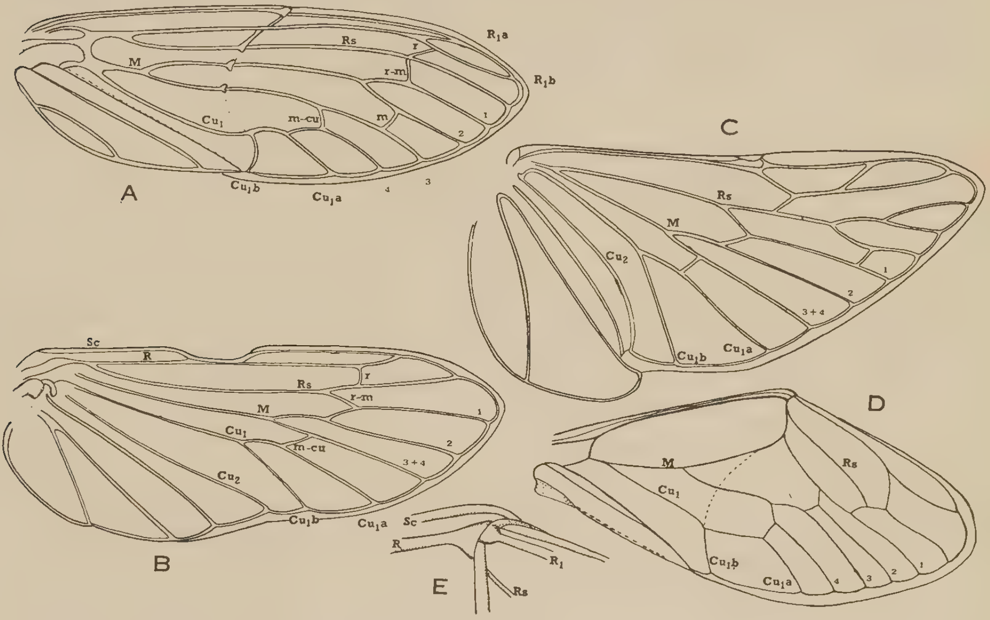

Fig. 24.—*A*, *Tettigarcta crinita; B*, *T. crinita; C*, *Cystosoma saundersi; D*, *Froggattoides typicus; E*, *F. typicus.*

Superfamily **PSYLLOIDEA**

The family name Protopsyllidiidae was proposed by Carpenter (1931) to comprise the genera *Protopsyllidium* Tillyard, *Permopsyllidium* Tillyard, and *Permothea* Tillyard. Since that date many further genera have been added by Davis (1942) and the present author (1943). Fossil psyllids have been placed also in the families Pincombeidae Tillyard and Psyllidae Latreille. Heslop-Harrison at one time (1951) preferred to regard Permian forms as belonging to the same family as recent ones.

It is not considered that the Archescytinidae are directly ancestral to psylloids, but since they are the earliest known Homoptera it is of interest to compare the venation of the two groups.

A comparison between the venation of the forewing of the archescytinid *Permopsylla permiana* (Fig. 1*B*) and *Psocopsyllidium media* (Fig. 25*B*) discloses close correspondence between the two wings. R_1b is absent from this particular psylloid tegmen, but as will be seen from other illustrations in Figure 25, it is usually present. In both tegmina M has been reduced to M_1, M_2, and M_{3+4}. The principal differences between the two tegmina are in the size of the clavus and in the fact that M arises from Cu_1 distally of the point where the basal bend of Cu_1 meets R.

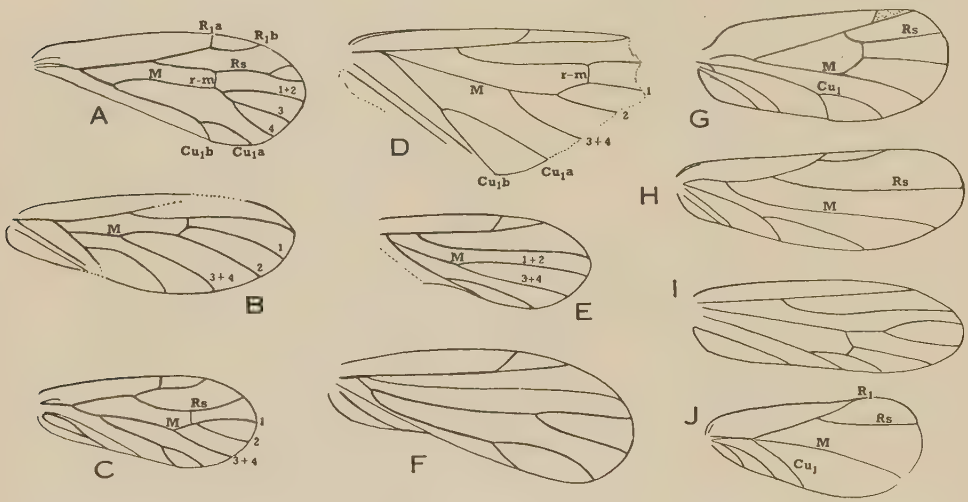

Fig. 25.—*A, Psocoscytina bifida; B, socopsyllidium media; C, Permotheëlla scytinopteroides; D, Pincombea mirabilis; E, Protopsyllidium sinuatum; F, Triassothea analis; G, Eopsyllidium delicatulum; H, Tripsyllidium wadei; I, Archipsylla liasina; J, Eupincombea postica.*

Figure 25*D* (*Pincombea mirabilis*) should next be compared with Figure 1*E* (*Sojanoscytina latipennis*). Carpenter (1939) has suggested that the wing of the latter is not that of an archescytinid, and reasons for differing with this view have already been given.

If the anomalous development of *Rs* in *Sojanoscytina mirabilis* is ignored, it will be seen that the 2 wings are remarkably similar.

It is not suggested that this venational resemblance between the two groups indicates close affinity, and the convergence may be due to the action of selection for flight efficiency purposes on the wing supports of groups of insects which share a common basic venational pattern. All psylloids are small insects, and none more than 5 mm in length.

The venation of the Protopsyllidiidae has been discussed recently by Heslop-Harrison (1955*a*). According to him the veins in Figure 25*B*, which are labelled M_1 and M_2 are in fact MA_{1+2} and MA_{3+4}, while the vein labelled M_{3+4} is *MP*. In a more recent paper (1955*b*) the same author figures the wing of a psyllid with a nodal line. This is of considerable interest and might seem to suggest that psyllids were derived from a prosbolid stock. Such a line of descent is improbable in view of differences in other structural features. It is more likely that a transverse line of weakness was already developed in the forewings of certain Protohomoptera. In the same paper, Heslop-Harrison has given "a hypothetical basic plan of homopterous venation". This, as has already been mentioned, is derived from the venational pattern of a specialized prosbolid, a family which in his opinion is more primitive than the earlier Archescytinidae.

Family **PROTOPSYLLIDIIDAE** Carpenter

PERMOPSYLLIDIUM AFFINE Tillyard

Permopsyllidium affine Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 28 (Upper Permian, New South Wales).

Permopsyllidium affine Tillyard, Evans, 1943, Rec. Aust. Mus. 21: 191.

The venation of this forewing, which in essential features is identical with that of *Permotheëlla scytinopteroides* (Fig. 25*C*), represents what may be regarded as the basic type of psylloid venation.

PERMOPSYLLIDIUM MITCHELLI Tillyard

Permopsyllidium mitchelli Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 28 (Upper Permian, New South Wales).

Permopsyllidium mitchelli Tillyard, Evans, 1943, Rec. Aust. Mus. 21: 191.

Very similar to *P. affine.*

PSOCOPSYLLIDIUM MEDIA Davis

Fig. 25*B*

Psocopsyllidium media Davis, 1942, Proc. Linn. Soc. N.S.W. 67: 115 (Upper Permian, New South Wales).

Psocopsyllidium media Davis, Evans, 1943, Rec. Aust. Mus. 21: 192.

Although the proportions of this wing are different from those listed above, the venation, apart from the possible absence of R_1a, is identical.

PERMOTHEELLA SCYTINOPTEROIDES Davis

Fig. 25*C*

Permotheëlla scytinopteroides Davis, 1942, Proc. Linn. Soc. N.S.W. 67: 116 (Upper Permian, New South Wales).

Permotheëlla scytinopteroides Davis, Evans, 1943, Rec. Aust. Mus. 21: 191.

It has already been mentioned that the venation of this wing is considered to be the most generalized of all known protopsyllids. It is not known whether the short vein indicated in the figure represents *Sc*. Attention is drawn to the *Y*-vein in the clavus. This development is, of course, of a specialized nature.

The venation of the wings of the six species that follow is essentially identical with that of those already listed:

PERMOPSYLLIDOPS STANLEYI Davis

Permopsyllidops stanleyi Davis, 1942, Proc. Linn. Soc. N.S.W. 67: 117 (Upper Permian, New South Wales).

CLAVOPSYLLIDIUM MINUTUM Davis

Clavopsyllidium minutum Davis, 1942, Proc. Linn. Soc. N.S.W. 67: 117 (Upper Permian, New South Wales).

PSYLLIDELLA MAGNA Evans

Psyllidella magna Evans, 1943, Rec. Aust. Mus. 21: 192 (Upper Permian, New South Wales).

PSYLLIDIANA DAVISIA Evans

Psyllidiana davisia Evans, 1943, Rec. Aust. Mus. 21: 192 (Upper Permian, New South Wales).

PROTOPSYLLOPS MINUTA Evans

Protopsyllops minuta Evans, 1943, Rec. Aust. Mus. 21: 192 (Upper Permian, New South Wales).

Lacking R_1a and resembling the wing of *P. media* (Fig. 25*B*) also in other respects. It is possible that both are hindwings.

BELPSYLLA RETICULATA Evans

Belpsylla reticulata Evans, 1943, Rec. Aust. Mus. 21: 193 (Upper Permian, New South Wales).

Two crossveins *r-m* are developed.

ARCHIPSYLLA LIASINA Handlirsch

Fig. 25*I*

Archipsylla liasina Handlirsch, 1906, Die Fossilen Insekten, p. 503 (Upper Lias, Germany).

This tegmen, from the Lias of Europe, resembles those from the Upper Permian of New South Wales listed above in the development of *M*. It differs from most of them in lacking R_1a and from all in the absence of *r-m* and the presence of *m-cu*. In the figure, which is after Handlirsch's illustration, the veins are shown as proximally separate. This is almost certainly incorrect.

TRIASSOPSYLLA PLECIOIDES Tillyard

Triassopsylla plecioides Tillyard, 1917, Proc. Linn. Soc. N.S.W. 42: 754 (Upper Triassic, New South Wales).

The holotype tegmen (in the Collection of the Australian Museum) has been examined. In Tillyard's illustration *Sc* is shown as a separate vein and crossveins are indicated between *R* and *Rs*. I have failed to find either and the venation of this wing is thus similar to Figure 25*C*.

PSOCOSCYTINA BIFIDA Davis

Fig. 25*A*

Psocoscytina bifida Davis, 1942, Proc. Linn. Soc. N.S.W. 67: 112 (Upper Permian, New South Wales).

Davis ascribed this forewing, which is 4 mm long, to the Scytinopteridae. He stated that it was distinguished from other genera in this family by the forked *Rs* and suggested that in general facies it resembled species in the genus *Orthoscytina*. It is here transferred to the Protopsyllidiidae because of the occurrence of a basal stalk comprising part of M_2 and part of Cu_1; also because of its small size. The forking of *R* is anomalous and of no significance, but if the branches of *M* are interpreted correctly then they represent a unique condition.

PROTOPSYLLIDIUM AUSTRALE Tillyard

Protopsyllidium australe Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 26 (Upper Permian, New South Wales).

In this and in the forewings that follow, *M* is reduced to 2 veins.

PROTOPSYLLIDIUM SINUATUM Davis

Fig. 25*E*

Protopsyllidium sinuatum Davis, 1942, Proc. Linn. Soc. N.S.W. 67: 117 (Upper Permian, New South Wales).

Protopsyllidium sinuatum Davis, Evans, 1943, Rec. Aust. Mus. 21: 191.

The 2 branches of *M* are interpreted as indicated because their point of separation lies closer to the base of the tegmen than the apex.

PERMOTHEA LATIPENNIS Tillyard

Permothea latipennis Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 28 (Upper Permian, New South Wales).

In Tillyard's illustration of the wing of this species he indicates a separate *Sc*, an *M* with 3 branches, and Cu_1 basally bent towards and meeting M_1 but also curving towards Cu_2. The type specimen (in the Collection of the Australian Museum) has been examined and it has been found that Tillyard's figure is incorrect and the venation of this wing is similar to those of others included in this series. A minor anomaly is an accessory vein associated with Cu_1.

PERMOPSYLLOIDES INSOLITA Evans

Permopsylloides insolita Evans, 1943, Rec. Aust. Mus. 21: 193 (Upper Permian, New South Wales).

This species is known only from a poorly-preserved specimen. The forewing has probably a 2-branched *M* and is of unusual shape.

Genus TRIASSOTHEA, gen. nov.

In the forewing *Rs* arises from *R* adjoining the stalk of *M* and Cu_1. *M* has 2 branches which separate from the main stem distally of where R_1a meets the costal border. The clavus is small and has a single anal vein.

Type species *Triassothea analis*, sp. nov.

Triassothea resembles *Protopsyllidium* in venation, but differs in the ratio of the length of the arms of *M* in relation to the length of its stalk.

TRIASSOTHEA ANALIS, sp. nov.

Fig. 25*F*

Length of forewing 2.8 mm; greatest width 0.8 mm. Holotype forewing C1590, Department of Geology Collection, University of Queensland, Mt. Crosby, Queensland (Upper Triassic).

This is the first wing of a protopsyllid to be recorded from Triassic strata. It resembles Permian forms in the series listed above. There are several other specimens from Mt. Crosby in the Geology Department Collection of the University of Queensland as follows: P62A (2 mm); C2109 (3.5 mm); C1738 (3.5 mm); C2110 (3 mm); C1955 (3 mm); C2107 (3 mm); C1766 (3 mm); C1596 (3 mm); C2062 (3 mm); C1608 (2.8 mm); C2111 (2.8 mm).

It is of interest to note that only one species is represented in the Mt. Crosby beds which thus differ from those of Permian strata at Belmont, New South Wales, which have a rich psylloid fauna.

CICADELLOPSIS INCERTA Martynov

Cicadellopsis incerta Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 7: 107 (Lias, Russia).

This forewing, which Martynov regarded as of uncertain position, is certainly that of a psyllid. The venation resembles that of *T. analis* (Fig. 25*F*) apart from the fact that the 2 arms of *M* are longer and those of Cu_1 shorter.

LIADOPSYLLA GEINITZI Handlirsch

Liadopsylla geinitzi Handlirsch, 1939, Ann. naturh. (Mus.) Hofmus., Wien **49**: 147 (Lias, Dobbertin).

This forewing was ascribed by Handlirsch to the family Psyllidae. R_1a is lacking, *M* has 2 branches, and the stalk of *M* and Cu_1 is longer than the distance between from where *M* separates from Cu_1 and Cu_1 branches.

LIADOPSYLLA TENUICORNIS Martynov

Liadopsylla tenuicornis Martynov, 1926, Bull. Acad. Sci. U.R.S.S. **20**: 1359 (Jurassic, Russia).

This forewing resembles those of recent psyllids in having R_1a meeting the costal margin close to its base. R_1b and Rs are of approximately equal length and M has 2 branches. Martynov placed this genus in a new family, the Liadopsyllidae.

Family **PINCOMBEIDAE** Tillyard

PINCOMBEA MIRABILIS Tillyard

Fig. 25*D*

Pincombea mirabilis Tillyard, 1922, Proc. Linn. Soc. N.S.W. **47**: 281 (Upper Permian, New South Wales).

Pincombea mirabilis Tillyard, 1926, Proc. Linn. Soc. N.S.W. **51**: 25.

This family was created by Tillyard in 1922 for the reception of this wing, which he considered to be a forewing, though it might well be a hindwing. Figure 25*D* has been drawn from the type specimen (in the Collection of the Australian Museum). It differs from Tillyard's illustration in respect to R and the omission of Sc. The principal special venational characteristic is the meeting basally of R, M, and Cu_1. Such a condition occurs also in certain recent psyllids (e.g. *Trioza chenopodii* Reuter (Heslop-Harrison 1951)).

EUPINCOMBEA POSTICA Davis

Fig. 25*J*

Eupincombea postica Davis, 1942, Proc. Linn. Soc. N.S.W. **67**: 114 (Upper Permian, New South Wales).

This is almost certainly a hindwing and suggests that the divergence from a common centre of the 3 principal veins may well be a characteristic of the venation of the hindwings of certain protopsyllids and not one meriting family differentiation.

PROTOPINCOMBEA OBSCURA Evans

Eopsyllidium delicatulum Davis, 1942, Proc. Linn. Soc. N.S.W. **67**: 114 (Upper Permian, New South Wales).

The venation of this wing resembles that of *Pincombea mirabilis* in general features. It differs in having 2 instead of 1 crossvein *r-m* and in having an additional crossvein between M and Cu_1.

PSYLLOIDEA OF UNCERTAIN POSITION

EOPSYLLIDIUM DELICATULUM Davis

Fig. 25*G*

Protopincombea obscura Evans, 1943, Rec. Aust. Mus. **21**: 193 (Upper Permian, New South Wales).

Davis provisionally ascribed this wing to the Permopsyllidae (= Protopsyllidiidae) and suggested that it might be a hindwing. He drew attention to the unusual feature of the basal separation of Cu_1 from R and to the absence of an association of Cu_1 with M. It is suggested either that this is a hindwing of a protopsyllid or else not the wing of a representative of the Psylloidea.

Genus TRIPSYLLIDIUM, gen. nov.

In a wing, which may be either a fore- or a hindwing, R_1a meets the costal border in a medial position, R_1b terminates midway between R_1a and the apex of the wing, and Rs terminates in the centre of the apex of the wing. M is a single vein. There are no crossveins and the clavus is small with a single anal vein.

Type species *Tripsyllidium wadei*, sp. nov.

TRIPSYLLIDIUM WADEI, sp. nov.

Fig. 25*H*

Length of wing 3 mm; greatest width 1 mm. Holotype wing F30980, Australian Museum Collection, Warner's Bay, N.S.W. (Upper Permian).

The remarks made concerning the wing of *E. delicatulum* apply to this one also.

The two species that follow are known from head impressions only:

PERMOCEPHALUS KNIGHTI Evans

Permocephalus knighti Evans, 1943, Trans. Roy. Soc. S. Aust. 67: 8 (Upper Permian, New South Wales).

Permocephalus knighti Evans, 1943, Rec. Aust. Mus. 21: 194.

PERMOCAPITUS GLOBULUS Evans

Permocapitus globulus Evans, 1943, Rec. Aust. Mus. 21: 194 (Upper Permian, New South Wales).

Superfamily **APHIDOIDEA**

Genus TRIASSOAPHIS, gen. nov.

The forewing has a strong principal convex vein parallel with the costal margin. In this vein are incorporated basally all the veins of the wing excepting Sc. Sc is present as a concave vein and terminates midway along the costal margin. The membrane of the wing is thickened between the apex of Sc and R. Rs is short, and M has 3 branches, M_1, M_2, and M_{3+4}. Cu_1 has 2 branches and Cu_1a reaches the wing margin at its widest part. The claval suture is obsolete.

Type species *Triassoaphis cubitus*, sp. nov.

TRIASSOAPHIS CUBITUS, sp. nov.

Fig. 26

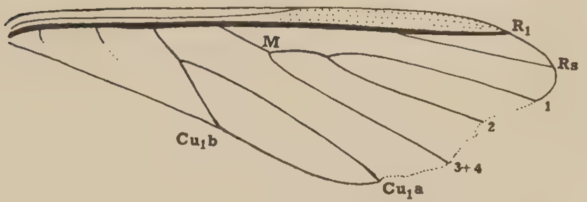

Fig. 26.—*Triassoaphis cubitus.*

Length of forewing 6 mm; greatest width 2 mm. Holotype forewing C2235, Department of Geology Collection, University of Queensland, Mt. Crosby, Queensland (Upper Triassic).

This is the first aphid to be described from Triassic strata. At first sight the venation would seem to differ in one respect only from that of recent aphids—the 2-branched condition of Cu_1. As, however, Cu_2 would seem to be obsolete in *T. cubitus,* or else incorporated in Cu_1, it is possible that this difference is more apparent than real and the vein labelled *Cu* in Patch's figure (Patch 1909) may in fact be Cu_1a and the one labelled 1*A* may be Cu_1b.

GENAPHIS VALDENSIS (Brodie)

Aphis valdensis Brodie, 1845, Fossil Insects, 33: 120 (Jurassic, England).
Genaphis valdensis (Brodie), Handlirsch, 1906, Die Fossilen Insekten, p. 643.

This wing also has a 3-branched *M* but Cu_1b is apparently lacking.

Superfamily **FULGOROIDEA**

It has been stated earlier, that while no difficulty attends the recognition of recent cercopoid tegmina, this does not apply to fossil forms. Such an ease of recognition of recent wings combined with difficulty of determination of fossil ones applies even more strongly to the Fulgoroidea.

Many authors have ascribed wings to this superfamily which doubtfully belong here or have claimed fulgoroid relationships where, in my opinion, none exist.

Tillyard (1919) derived the Fulgoroidea from the Scytinopteridae. Later (1922) he quoted Muir as suggesting that the Prosbolidae were archaic fulgoroids and at the same time transferred various genera, which he had previously placed in the Scytinopteridae, to the Trophiduchidae and Cixiidae. In 1926 (Tillyard 1926*b*) he transferred one of these genera (*Mesodipthera*) from the Trophiduchidae to the Prosbolidae and stated that this family would appear to have been ancestral to recent fulgoroids.

Martynov (1928) regarded his genus *Permocixius* as a cixiid and in 1935 ascribed *Prosbolopsis* Martynov to the Fulgoroidea. Finally, Bekker-Migdisova (1940, 1946, 1948) considered the Scytinopteridae to be a family of the Fulgoroidea. Her views are based, not solely on a consideration of wing venation, but also on the structure of the rest of the body and in particular the head.

Early association of forewings to this superfamily was due, in part, to failure to appreciate that a *Y*-vein in the clavus is not a development which is confined to the Fulgoroidea (Evans 1943). Further confusion is associated with difficulties of venational interpretation of veins subject to secondary proliferation.

Previously (Evans 1948), I have followed Fennah's (1944) interpretation of fulgoroid venation and have accepted his view that a separate *Sc* lies between *R* and the costal margin. Recently Heslop-Harrison (1955*b*) has suggested that the venation of the Fulgoroidea is basically identical with that of the rest of the Homoptera. While for some wings Heslop-Harrison's interpretation is acceptable, for others it would seem to be incorrect and for this reason I have found it impossible to reach a decision on which of the two conflicting viewpoints is correct.

The forewing of a New Zealand cixiid (*Oliarus atkinsoni* Myers) is illustrated in Figure 28*A*. If this wing is compared with that of *Permocicadopsis angustata,* the following differences will be noted: all the veins, apart from Cu_1 and the anal veins, are, in the cixiid, divided ante-apically into 2 parts; the arms of Cu_1 are very long; there is a crossvein between the 2 branches of Cu_1; *M* has 3 instead of 4 branches; the anal veins form a *Y*-vein.

In spite of these differences between the 2 tegmina, it is not easy to determine those features of the cixiid wing which may be regarded as characteristic. While, for instance, *Rs* diverges from *R* and Cu_1 separates into Cu_1a and Cu_1b at one-third of the length of the wing from the base, in the forewings of many other unrelated Homoptera such a similar proximal vein separation also occurs. Furthermore, a tendency towards vein-splitting, the development of additional crossveins, and a *Y*-vein in the clavus are features found also in other groups besides the Fulgoroidea. It would seem that the only special characteristic of the wing of *O. atkinsoni* is associated with Cu_1. The length of the 2 arms of this vein has already been mentioned, but another fulgoroid peculiarity is that Cu_1b as well as Cu_1a may extend to the apex of the wing and the former may be widely separated apically from the apex of the claval suture.

If Figure 28*A* were labelled in accordance with Fennah's interpretation, then the vein indicated as R_1 would be *Sc* and *Rs* would become *R*.

It is accepted that *Sc* may be separate from the costal margin in fulgoroids, as indicated in Figures 27*A* and 27*B*. It is, however, always basally distinct from *R* as would be expected from Fennah's study of the precursory tracheae.

Bekker-Migdisova has based her opinion that the Scytinopteridae are a family of the Fulgoroidea on cephalic, as well as on venational, characterisics. Previously (Evans 1948) I have stated that the head of *Scytinoptera cubitalis*, figured by Bekker-Migdisova, does not have a single significant feature which suggests fulgoroid affinities. Moreover, the only venational one common to the two groups is a *Y*-vein in the clavus. The Fulgoroidea are undoubtedly an old group and will, very probably, have developed their distinctive features as early as Permian times. The fact that no undoubted fossil remains are known from before the Mesozoic, though surprising, is almost certainly of no significance.

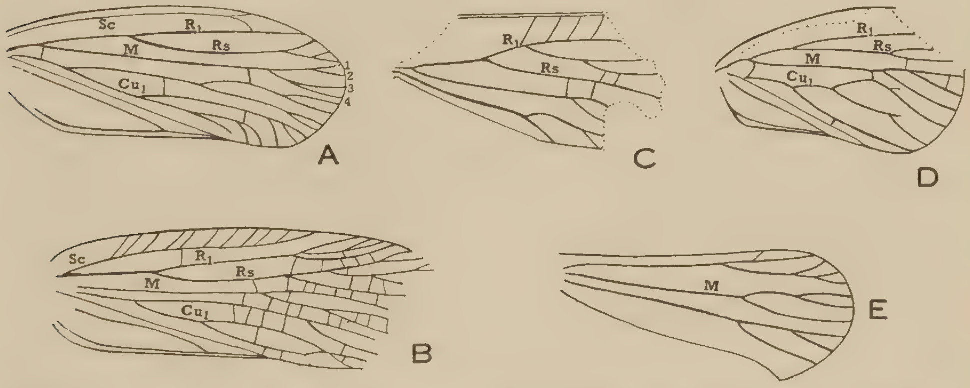

Fig. 27.—*A*, *Fulgoridium pallidum*; *B*, *Eofulgoridium kisylkinense*; *C*, *Triassocixius australicus*; *D*, *Elasmocoelidium rotundatum*; *E*, *Eofulgoridium proximum*.

TRIASSOCIXIUS AUSTRALICUS Tillyard

Fig. 27*C*

Triassocixius australicus Tillyard, 1919, Proc. Linn. Soc. N.S.W. **44**: 878 (Upper Triassic, Queensland).

The forewing may either be that of a fulgoroid, or else of a scytinopterid with accessory veins. It is here placed in the Fulgoroidea because of the presence of a vein lying between R_1 and *Rs*, as this is a condition which is unknown in the Scytinopteridae (see Figs. 4, 5).

MESOCIXIUS TRIASSICUS Tillyard

Mesocixius triassicus Tillyard, 1919, Proc. Linn. Soc. N.S.W. **44**: 877 (Upper Triassic, Queensland).

This wing is ascribed to the Fulgoroidea for the same reason as given for *T. australicus*.

ELASMOCOELIDIUM ROTUNDATUM Martynov

Fig. 27*D*

Elasmocoelidium rotundatum Martynov, 1926, Bull. Acad. Sci. U.R.S.S. **20**: 1355 (Jurassic, Turkestan).

There is no doubt that this is a fulgoroid wing because of the combination of the features of a *Y*-vein in the clavus and the length of the arms of Cu_1.

EOFULGORIDIUM KISYLKINENSE Martynov

Fig. 27*B*

Eofulgoridium kisylkinense Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 7: 95 (Lias, Russia).

This wing is figured to show how *Sc* may be retained in the Fulgoroidea.

FULGORIDIUM PALLIDUM Handlirsch

Fig. 27*A*

Fulgoridium pallidum Handlirsch, 1906, Die Fossilen Insekten, p. 497 (Upper Lias, Germany).

This wing is figured because, not only has it a separate *Sc*, but also because it displays another feature peculiar to the forewings of many fulgoroids. This is the development of more accessory veins in association with Cu_1 than with the other veins.

EOFULGORIDIUM PROXIMUM Martynov

Fig. 27*E*

Eofulgoridium proximum Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 7: 97 (Lias, Russia).

This hindwing is a further example of the trend mentioned above since *M* has reduced venation whilst Cu_1 has acquired an additional branch.

No useful purpose would be served by listing all the several undoubted Mesozoic fulgoroid wings which have been figured and described by Handlirsch (1906, 1913, 1939). These number over 70 and none would seem to have any features that call for special comment.

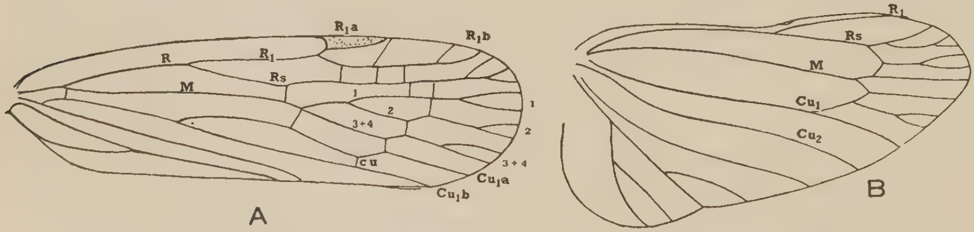

Fig. 28.—*A*, *Oliarus atkinsoni*; *B*, *Achilus flammeus.*

HOMOPTERA OF UNCERTAIN POSITION

The species listed below are represented by poorly-preserved fragments, hence cannot be placed with any certainty. The two species marked with an asterisk are only doubtfully Homoptera:

Archijassus minimus Martynov, 1926, Bull. Acad. Sci. U.R.S.S. **20**: 1349.
Archijassus minutus (Heer), Handlirsch, 1906, Die Fossilen Insekten, p. 502.
Archijassus morio (Heer) Handlirsch, 1906, Die Fossilen Insekten, p. 502.
Archipsylla primitiva Handlirsch,* 1906, Die Fossilen Insekten, p. 503.
Atitizon jassoides Handlirsch, 1939, Ann. naturh. (Mus.) Hofmus., Wien **49**: 144.
Cercopidium mimas Westwood, Handlirsch, 1906, Die Fossilen Insekten, p. 653.
Cercopidium schäfferi Westwood, Handlirsch, 1939, Ann. naturh. (Mus.) Hofmus., Wien **49**: 163.
Cicada ? lowei Etheridge & Olliff, 1890, Mem. Geol. Surv. N.S.W., Palaeontology, **1890**: 7.
Cyclostina delutinervis Martynov, 1926, Bull. Acad. Sci. U.R.S.S. **20**: 1350.
Diptheropsis incerta Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. **7**: 110.
Eojassus indistinctus Handlirsch, 1939, Ann. naturh. (Mus.) Hofmus., Wien **49**: 145.
Fulgoropsis dubiosa Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. **7**: 97.
Homopterites anglicus Handlirsch, 1906, Die Fossilen Insekten, p. 500.
Karabasia paucinervis Martynov, 1926, Bull. Acad. Sci. U.R.S.S. **20**: 1357.
Karrajassus crassinervis Martynov, 1926, Bull. Acad. Sci. U.R.S.S. **20**: 1352.
Kisylia psylloides Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. **7**: 109.
Margaroptilon woodwardi Handlirsch, 1906, Die Fossilen Insekten, p. 499.
Margaroptilon bulleni Handlirsch, 1906, Die Fossilen Insekten, p. 499.
Margaroptilon germanicum Handlirsch, 1939, Ann. naturh. (Mus.) Hofmus., Wien **49**: 141.
Mesaleuropsis venosa Martynov, 1937, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. **7**: 108.
Mesocixoides brachyclada Tillyard, 1922, Proc. Linn. Soc. N.S.W. **47**: 463.
Mesodipthera grandis Tillyard, 1919, Proc. Linn. Soc. N.S.W. **44**: 873.
Mesoscytina affine Tillyard, 1919, Proc. Linn. Soc. N.S.W. **44**: 871.
Orthoprosbole congesta Martynov,* 1935, Bull. Acad. Sci. U.R.S.S., Class. Sci. Math. et Nat., p. 445.
Permodiptheroides dubitans Martynov, 1928, Trav. Mus. Geol. U.R.S.S. **4**: 37.
Procercopsis coriacea Handlirsch, 1939, Ann. naturh. (Mus.) Hofmus., Wien **49**: 141.

WINGS OF CARBONIFEROUS INSECTS ASCRIBED TO THE HOMOPTERA

BLATTINOPSIS RETICULATA (Germar)

Handlirsch, 1906, Die Fossilen Insekten, p. 158.

Haupt (1929) has stated that this is a homopterous wing. I have previously (1948) disputed this and am still of the same opinion.

DICTYOCICADA ANTIQUA Brogniart

Handlirsch, 1906, Die Fossilen Insekten, p. 325.

Heslop-Harrison (1955*a*) is of the opinion that this is the wing of a homopteron. This is very doubtful but, even if correct, is of little significance as the venation is so specialized as not to be informative.

PSEUDOFULGORA EBERSI (Dohrn)

Handlirsch, 1906, Die Fossilen Insekten, p. 347.

This wing, which has been ascribed to the Protoblattoidea, though certainly not of a homopteron, is of interest, since not only are costal and claval sutures developed, but there is also an apparent nodal line.

RECULA PARVA (Schlechtendal)

Handlirsch, 1906, Die Fossilen Insekten, p. 128.

Haupt (1929) has suggested that this wing may be that of an insect ancestral to the Cercopidae. Previously (Evans 1948) I have agreed that it may have homopterous affinities.

Suborder HETEROPTERA

In a table given by Hennig (1953, Fig. 12) in which the periods of origin of the various insect orders are shown, the Heteroptera, as well as the Homoptera, of the Permian are indicated as having been derived from the Lower Permian Paleorrhyncha. The Archescytinidae (the Paleorrhyncha are not recognized as a separate series of the Homoptera) almost certainly will not have been ancestral to the Heteroptera. Nevertheless it is very probable that already by Lower Permian times true Heteroptera will have been in existence. While these may have resembled contemporary Homoptera, so far as wing venation is concerned, their head-shape and other characteristics will have been different.

Tillyard, in 1926, described a tegmen from the Upper Permian of New South Wales which he named *Actinoscytina belmontensis* and which he placed in the family Scytinopteridae. His illustration of *A. belmontensis* is reproduced in Figure 29*B,* though his reconstruction of the missing parts of the wing has been omitted. In his description of the genus Tillyard pointed out that it represented a somewhat isolated type and could be distinguished by R_1a and Rs arising from the same point and by the arrangement of the distal branches of M and Cu_1, as straight, slightly diverging rays.

Among the fossils from Mt. Crosby are very numerous tegmina of insects that must have been closely related to *A. belmontensis,* also the remains of two almost complete insects. This abundant material, together with an additional almost complete tegmen from the Upper Permian beds of New South Wales, enables a re-assessment to be made of the position of the type species and renders necessary the creation of a new family which is placed provisionally in the Heteroptera.

Family ACTINOSCYTINIDAE, fam. nov.

Hemiptera from Upper Permian and Triassic strata of Australia and from the Lias of Europe ranging in length from 3 to 6 mm, dorsoventrally flattened, and with the tegmina overlapping apically. *R, M,* and

Cu_1 are approximately parallel with each other and with the costal margin. R_1a, which is absent from all but one of the known tegmina from Triassic strata, when present, arises from R at, or near, to the same point as Rs.

ACTINOSCYTINA BELMONTENSIS Tillyard

Figs. 29*A*, 29*B*

Actinoscytina belmontensis Tillyard, 1926, Proc. Linn. Soc. N.S.W. 51: 18 (Upper Permian, New South Wales).

The holotype tegmen is illustrated in Figure 29*B*. The tegmen shown in Figure 29*A* is ascribed to this species although differing from the holotype in certain particulars. Thus Rs arises from R distally of R_1a; Cu_1a is differently shaped and so also is the apex of the tegmen. The vein extending from the claval suture to the apex of the tegmen which is, as shown in Figure 29*A*, joined to Cu_1b, is of uncertain derivation. It is possible that it is not a vein but the wing margin, the apparent margin being in the nature of an appendix.

F41384 (Fig. 29*A*), Australian Museum Collection. Warner's Bay, N.S.W. (Upper Permian). Length 6 mm, greatest width 2 mm.

Genus PLATYSCYTINELLA, gen. nov.

The tegmina narrow apically to a varying degree. R_1a is absent. Crossvein *r-m* is nearer to the apex of the tegmen than the angled transverse vein joining the apices of M and Cu_1. The straight line continuation of M to the apex of the tegmen is by way of its anterior branch.

Type species *Platyscytinella paradoxa,* sp. nov.

This genus differs from *Actinoscytina* Tillyard in the venational features described above.

PLATYSCYTINELLA PARADOXA, sp. nov.

Figs. 29*C-E*, 29*I-K*

Length of holotype tegmen 3.2 mm; greatest width 1 mm. Holotype tegmen C169 (Fig. 29*J*) Department of Geology Collection, University of Queensland, Mt. Crosby, Queensland (Upper Triassic). Additional specimens: C1906 (Fig. 29*C*), length 5.8 mm; C1587 (Fig. 29*D*), 3 mm; C1580 (Fig. 29*E*), 3 mm; C155 (Fig. 29*I*), 3 mm; C1658 (Fig. 29*K*), 2.5 mm; and unfigured specimens C1904, 3 mm; C1613, 3 mm; C1583, 3 mm; C1604, 3 mm.

Genus HETEROSCYTINA, gen. nov.

The tegmina narrow apically. R_1a may be present or absent. Crossvein *r-m* is in alignment with the transverse vein that links the apices of M and Cu_1 and continues as far as the hind margin of the tegmen. In the clavus 1*A* is close to, and parallel with, the claval suture while 2*A* adjoins and is parallel with the hind margin of the tegmen.

Type species *Heteroscytina tillyardi*, sp. nov.

This genus differs from *Platyscytinella* in the development of the post-apical composite transverse vein.

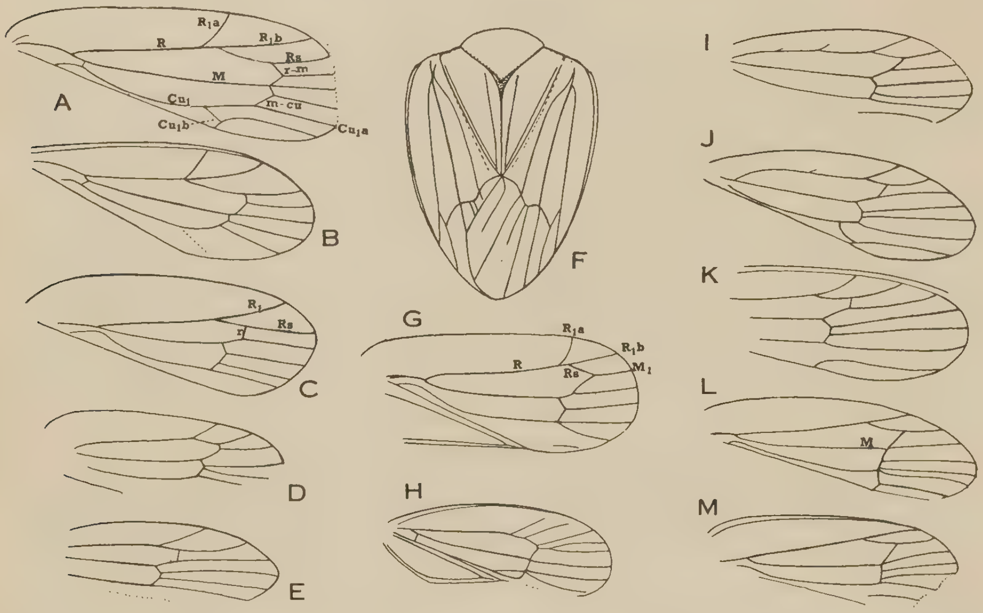

Fig. 29.—*A*, *Actinoscytina belmontensis*; *B*, *A. belmontensis*; *C*, *Platyscytinella paradoxa*; *D*, *P. paradoxa*; *E*, *P. paradoxa*; *F*, *Heteroscytina tillyardi*; *G*, *Triscytina rotundata*; *H*, *Cercopinus ovalis*; *I*, *Platyscytinella paradoxa*; *J*, *P. paradoxa*; *K*, *P. paradoxa*; *L*, *Heteroscytina tillyardi*; *M*, *H. tillyardi*.

HETEROSCYTINA TILLYARDI, sp. nov.

Figs. 29*F*, 29*L*, 29*M*

Length of holotype tegmen 4 mm; greatest width of whole insect 3 mm. Holotype tegmen C691 (Fig. 29*F*), Department of Geology Collection, University of Queensland, Mt. Crosby, Queensland (Upper Triassic). Additional specimens: C972 (Fig. 29*L*), length 4 mm; C1879 (Fig. 29*M*), 2 mm; and unfigured specimens C1578, 3 mm; C2113, 3.5 mm; C1659, 3 mm; C1655, 3 mm; C1571, 3 mm; C1797, 3 mm.

Genus TRISCYTINA, gen. nov.

The apex of the tegmen is evenly rounded. R_1a is present and $Rs + (?) M_1$ form a single vein apically. In the clavus 1*A* is adjacent to the claval suture and 2*A* lies alongside the hind margin of the tegmen.

Type species *Triscytina rotundata*, sp. nov.

Triscytina differs from other genera in the Actinoscytinidae in the absence of *r-m* and in the shape of the tegmen.

TRISCYTINA ROTUNDATA, sp. nov.

Fig. 29*G*

Length of tegmen 3 mm; greatest width 1.2 mm. Holotype tegmen C2311, Department of Geology Collection, University of Queensland, Mt. Crosby, Queensland (Upper Triassic).

The following fossil insects from the Lias of Dobbertin, which were placed by Handlirsch (1939) in the family Procercopidae, would appear to belong to the Actinoscytinidae and are accordingly transferred to this family:

Cercopinus ovalis Handlirsch (Fig. 29*H*), 1939, Ann. naturh. (Mus.) Hofmus., Wien 49: 143, Pl. 16, fig. 295.
Archicercopis falcata Handlirsch, op. cit., Pl. 15, fig. 291, p. 142.
Cercoprisca similis Handlirsch, op. cit., Pl. 16, fig. 297, p. 143.
Eocercopis ancyloptera Handlirsch, op. cit., Pl. 16, fig. 294, p. 143.

DISCUSSION OF THE ACTINOSCYTINIDAE

Tillyard (1936) in a note in *Nature* reporting the discovery of the Mt. Crosby beds, mentioned and illustrated the tegmen of an insect (see Fig. 18*B*) which he described as that of "a specialized scytinopterid type in process of becoming a true heteropterous type". This suggests that the only significant differences existing between insects in the two suborders of the Hemiptera are to be found in the forewing, or that changes in the forewing are necessarily associated with others affecting the head and other parts of the body.

While it may be assumed that early Heteroptera had a similar venational pattern to that of early Homoptera, though they will have differed in other respects, such wings as exhibit progressive divergence from this basic pattern cannot be interpreted as providing an indication that their bearers were "becoming Heteroptera".

The tegmen of *Platyscytinella paradoxa* (Fig. 29*C*) is not very different in venational features from those of certain scytinopterids, e.g. *S. kokeni* and *S. maculata* (Figs. 3*E*, 3*F*). In all 3 tegmina *R* and *M* have a common proximal origin, R_1a is absent, *r-m* is present, Cu_1 is bent towards $R + M$ near the base of the tegmen, and there are apparently the same number of short apical branches of *M* and Cu_1. Furthermore, although *S. maculata* has a clavus with separate anal veins, a *Y*-vein was developed in the clavus of related forms (e.g. *S. reducta*, Fig. 3*D*).

In spite of this resemblance there are five separate features in the tegmina of the Actinoscytinidae, which if taken together, suggest that these wings were those of insects belonging to the Heteroptera. These are as follows: a progressive tendency for the apex of the tegmen to become flexible. This characteristic is one which would seem to have been induced by selection in most groups of Heteroptera. In the tegmina of most Homoptera the 2 apical branches of Cu_1 are almost invariably retained and readily recognizable. The identity of the branches of Cu_1 are difficult to determine in the Actinoscytinidae in spite of the range of different forms available for study. Nevertheless, the termination of this vein suggests a heteropterous rather than a homopterous development. While in the Permian species (*Actinoscytina belmontenis,* Figs. 29*A*, 29*B*) the identity of the veins beyond the post-apical crossveins can be determined, it would not be possible to identify the corresponding veins in *Heteroscytina tillyardi* (Figs. 29*F*, 29*L*, 29*M*) had not the earlier forms been available for comparison. This condition of the apical veins is one common to most Heteroptera where the veins supporting the apex of the forewing are, in part, of uncertain origin. The remaining heteropterous characteristics are a dorsoventrally flattened body with apically overlapping tegmina and the condition of the clavus. Among the numerous specimens available for study only two had the clavus intact, which suggests a deep claval suture, and the 2 anal veins lie close to the claval suture and the hind margin of the tegmen respectively.

Family **IPSVICIIDAE** Tillyard

In 1919 Tillyard created the family Ipsviciidae for the reception of species based on 3 tegmina from the Upper Triassic of Queensland which he named *Ipsvicia jonesi, I. maculata,* and *I. acutipennis.* These 3 tegmina resemble each other so closely that they could well have been ascribed to a single species and the salient features common to all are shown in Figure 30*A*. The tegmen, as described by Tillyard, is rugose and pitted. It narrows apically, lacks *Rs,* has *M* and Cu_1 forming a single vein proximally, and a *Y*-vein is developed in the clavus. In Tillyard's illustrations of the tegmina of *I. jonesi* and *I. maculata* but not of *I. acutipennis,* there is a transverse vein, or suture, which extends from the point of function of *R* and $M + Cu_1$ to the costal border. Tillyard regarded this as *Sc.*

In 1923, the same author described two further species (Tillyard 1923) which he placed in the same family but in a different genus. These he named *Ipsviciopsis elegans* and *I. magna.* The wing of the former is illustrated in Figure 30*B*. The illustration is not a copy of Tillyard's figure but has been reproduced from a photograph of the holotype.

Figure 30*E* represents a fragment of a wing of a previously unrecorded specimen from the Triassic of Denmark Hill, Queensland (C2138, length 8 mm) which is ascribed also to *I. elegans* (Department of Geology Collection, University of Queensland).

It is suggested that the transverse furrow shown in Figures 30*A*, 30*B*, and 30*E* is homologous with one I have previously called the costal fracture (Evans 1950). The detached portion of the wing shown in Figure 30*A* lends support to this hypothesis.

Ipsviciopsis spp. differ from those in the genus *Ipsvicia* in having 2 instead of 1 longitudinal vein anterior of *M*. Tillyard identified these 2 veins as *R* and *Rs* respectively. The one closest to the costal margin lies in a depression and is concave while all the other veins of the wing are raised in relief. Heslop-Harrison (1955*a*), as well as previous authors, have pointed out that in the Hemiptera the convexity or concavity of veins does not provide an indication of their derivation. Nevertheless, as R_1 is usually a convex vein and *Rs* a concave one it seems probable that the 2 veins nearest the costal margin in *Ipsviciopsis elegans* are *Sc* and *R* respectively.

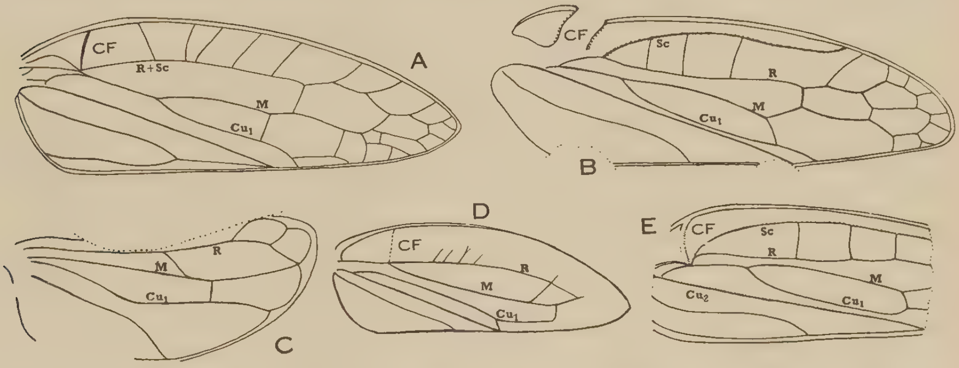

Fig. 30.—*A, Ipsvicia jonesi; B, Ipsvicopsis elegans; C, Ipsivicia jonesi; D, Paraknightia magnifica; E, Ipsviciopsis elegans.*

In 1923, Tillyard described a hindwing which he ascribed to his earlier species *Ipsvicia jonesi* (Fig. 30*C*), and in 1926 he described the Ipsviciidae as "early Fulgoroidea, probably ancestral to the Tettigometridae". Handlirsch (1939) while not questioning the inclusion of the Ipsviciidae in the Fulgoroidea, suggested that the hindwing ascribed to *I. jonesi* was more probably that of a jassid or cercopid.

In 1950, I transferred *Paraknightia magnifica* (Fig. 30*D*) from the Ipsviciidae, in which I had previously placed it, to a new family, the Paraknightiidae, which I regarded as a family of the Heteroptera.

The Ipsviciidae are now likewise transferred to the Heteroptera and are regarded as comprising two genera only, *Ipsvicia* Tillyard and *Ipsviciopsis* Tillyard. The genera *Stanleyana, Stenovicia, Permovicia,* and *Palaeovicia,* previously placed in the Ipsviciidae, are undoubtedly homopterous and have been considered elsewhere.

The reasons for this action follow: a costal fracture (see Evans 1950) is a heteropterous characteristic which is unknown in the Homoptera. No other known extinct or recent Homoptera has a tegminal venation in any way resembling that of the Ipsviciidae, yet the tegmina are undoubtedly those of Hemiptera. No Palaeozoic or Mesozoic Homoptera are known with hindwings having the venation reduced to the extent shown in Figure 30*C*.

Family **DUNSTANIIDAE** Tillyard

Tillyard in 1916 described an insect wing from the Triassic of Queensland which he named *Dunstania pulchra.* He regarded it as a hindwing and placed it in the family Dunstaniidae, order Lepidoptera. Later (1918*a*) he transferred this family to the Heteroptera and described 2 more Triassic wings as *Dunstaniopsis triassica* and *Paradunstania affinis.* The 3 wings are illustrated in Figure 31 and the drawings have been made from the type specimens and not copied from Tillyard's illustrations.

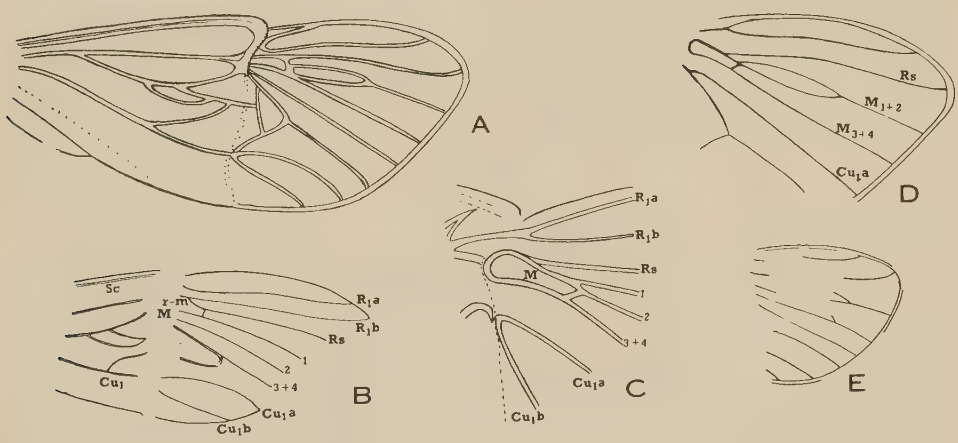

Fig. 31.—*A, Dunstania pulchra; B, Dunstaniopsis triassica; C, Dunstania pulchra; D, D. pulchra; E, Paradunstania affinis.*

In the actual fossil of *D. triassica* (Fig. 31*B*), the right-hand side of the wing is at a slightly higher level than the remainder and direct continuity between the veins of the 2 sides is not discernible. Figure 31*C* represents the base of the wing fragment of *Dunstania pulchra* (Fig. 31*D*) shown in greater detail.

Tillyard regarded the fragments of all 3 wings as parts of the forewing of a heteropteron and presented a reconstruction of his conception of a complete hemielytron (Fig. 31*A*) which he called *Dunstania pulchra.* In his textbook (1926*c*) he stated that the Dunstaniidae were ancestral to the Pentatomoidea.

This reconstruction has been reproduced in several textbooks, hence is well known, but a study of the several illustrations in Figure 31 suggests that it is based on a weak foundation of evidence. It is apparent that while the proximal part of the reconstruction of "*Dunstania pulchra*" is based on the corresponding portion of the wing of *Dunstaniopsis triassica,* the distal part, or membrane, is based anteriorly on the wing of *D. pulchra* and posteriorly on that of *D. triassica,* in spite of the fact that the venation of the upper distal part of the 2 wings is completely different!

It is possible that the identity of the veins as they are labelled in Figure 31 may be incorrect. These have been determined by reference to the fore- and hindwings of the Cicadomorphidae (Figs. 20, 21) in particular to the hindwing of *Fletcheriana triassica.* The crossvein *r-m* which links *Rs* with M_1 has been assumed to be homologous with the sole crossvein present in the wing of *D. triassica.*

Although Tillyard's reconstruction of the wing of *Dunstania pulchra* is not accepted, his placing of the family Dunstaniidae in the Heteroptera is probably correct.

OTHER TRIASSIC HETEROPTERA

TRIASSOCORIS MYERSI Tillyard

Triassocoris myersi Tillyard, 1922, Proc. Linn. Soc. N.S.W. 47: 466 (Upper Triassic, Queensland).

Triassocoris myersi Tillyard, 1923, Proc. Linn. Soc. N.S.W. 48: 494.

The special interest of this undoubtedly heteropterous wing is the presence of an apparent costal fracture. Three other *Triassocoris* spp. have been described by Tillyard, but they are based on too poorly-preserved and fragmentary material to be of any interest.

POLYCYTELLA TRIASSICA Tillyard

Polycytella triassica Tillyard, 1922, Proc. Linn. Soc. N.S.W. 47: 460 (Upper Triassic, Queensland).

This wing requires special mention because it bears a superficial resemblance to Heteroptera in the family Piesmidae. Tillyard ascribed it to the Scytinopteridae, but it would seem to belong to the family Jurinidae Zalessky, 1929, order Glosselytrodea Martynov, 1938 (Laurentiaux 1953).* It is possible that *Permoberothella perplexa* Riek (1953) from the Upper Permian of New South Wales, which was described as a neuropteron, may also belong to the Glosselytrodea.

POST-TRIASSIC HETEROPTERA

Numerous Jurassic and Cretaceous Heteroptera have been described by Handlirsch (1906, 1939) and other authors. Some of these wings provide evidence that already by Mesozoic times the venation of the Heteroptera had become extremely specialized, unlike that of the Homoptera which has remained remarkably stable.

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* Mr. Riek has drawn my attention to the fact that Martynova (1952, Trav. Inst. Paléozool. Acad. Sci. U.R.S.S. 40: 188) has previously ascribed *P. triassica* to the family Jurinidae.

INTERRELATIONSHIPS OF THE HOMOPTERA

In Figure 32 the author's present views on the possible interrelationships of most groups of Homoptera are indicated. Both known and conjectured periods of origin are also shown in the diagram, the latter being indicated by broken lines.

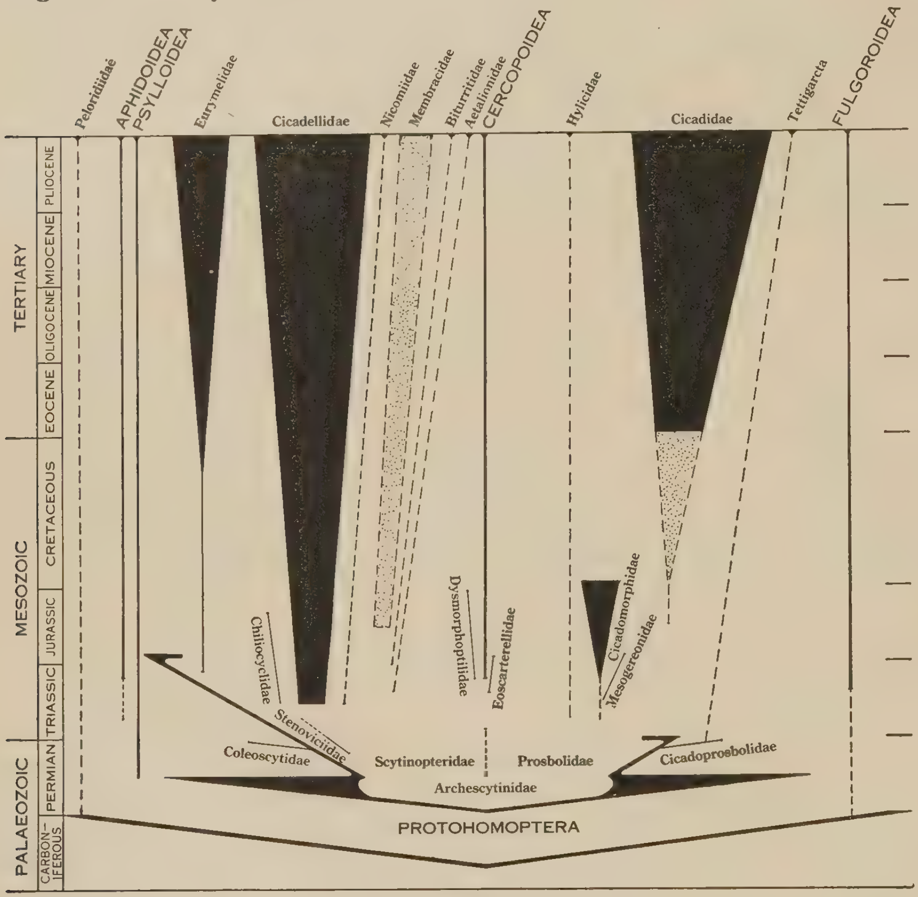

Fig. 32.

The Cercopoidea are of uncertain affinity and this uncertainty has been expressed by placing them in a central position. By this means it is intended to show that they may have been derived neither from the Scytinopteridae nor from the Prosbolidae. They would, however, appear to be a component of the Cicadomorpha (Evans 1951) and hence it would be misleading to place them in a position on the diagram similar to that given to the Fulgoroidea.

ACKNOWLEDGMENTS

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Appendix I

List of New Names

(*a*) *Families*

homoptera: Hylicellidae, Stenoviciidae, Chiliocyclidae, Eoscarterellidae, Cicadoprosbolidae, Cicadomorphidae.

heteroptera: Actinoscytinidae.

(*b*) *Genera and Species*

homoptera

Scytinopteridae: *Triassoscytina incompleta*, *Triassoscytinopsis stenulata*, *T. aberrans*, *T. paranotalis*, *Mesothymbris perkinsi*, *M. woodwardi*, *Mesonirvana abrupta*, *Triassoscelis anomala*, *Crosbella elongata*, *C. alata*, *Mesocicadella venosa*, *Triassocotis australis*, *Mesojassula marginata*.

Hylicellidae: *Hylicella colorata*, *H. reducta*.

Stenoviciidae: *Permocentrus*, gen. nov. (type species *Permoscarta trivenulata* Tillyard).

Chiliocyclidae: *Mesoledra*, nom. nov. for *Mesojassus* Handlirsch (type species *M. pachyneurus* Handlirsch), nec. *Mesojassus* Tillyard (type species *Mesojassus ipsviciensis* Tillyard).
Cercopidae: *Trifidella perfecta, Alotrifidus interruptus.*
Dysmorphoptilidae: *Dysmorphoptiloides elongata, D. parva.*
Eoscarterellidae: *Eoscarterella media, Eoscartoides bryani.*
Cicadomorphidae: *Fletcheriana triassica.*
Psylloidea: *Triassothea analis, Tripsyllidium wadei.*
Aphidoidea: *Triassoaphis cubitus.*

HETEROPTERA

Actinoscytinidae: *Platyscytinella paradoxa, Heteroscytina tillyardi, Triscytina rotundata.*

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